Responses to External Perturbations in Selected Human Motor Tasks

A Systematic Review and Analysis

TECHNISCHE UNIVERSITÄT DARMSTADT

Vom Fachbereich Humanwissenschaften
der Technischen Universität Darmstadt

zur Erlangung des Grades
Doctor philosophiae
(Dr. phil.)

Dissertation von
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Darmstadt, 2019

Tokur, Dario Sinan: Responses to External Perturbations in Selected Human Motor Tasks – A Systematic Review and Analysis.

Darmstadt, Technische Universität Darmstadt, Institut für Sportwissenschaft

Jahr der Veröffentlichung der Dissertation auf TUprints: 2019

Tag der mündlichen Prüfung: 15. Oktober 2019

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Darmstadt, den 22. April 2019

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Abstract

Balance is critical for human posture control when standing upright and during cyclic locomotor tasks such as walking or running, as well as for acyclic tasks such as gait initiation or complex sport movements. In the course of evolution, Homo sapiens developed an upright posture for bipedalism, thus freeing the upper limbs (arms) to interact with objects. Human upright stance is characterized by two straight legs and the center of mass (COM) is located above the hip, thus maximizing potential energy (due to high COM position) enabling great maneuverability for fast re-orientation of the body axis and re-direction of movement direction in space. Nevertheless, bipedalism is mechanically much more challenging (e.g. regarding stability) compared to other body morphologies in legged animals such as a quadrupedal leg configuration. This evolutionary innovation does not only provide benefits (such as those mentioned above), but also makes control functions difficult, which might involve instability of the whole mechanical system with segments arranged like an upside-down chain. To achieve the stable upright human stance and to prevent collapse, it is fundamental to continuously balance all segments above the feet by introducing appropriate joint torques and continuously adjusting the orientation of the ground reaction forces (GRF). Nevertheless, human motor control during tasks such as standing and walking provides stability in the case of external perturbations. Thus, humans are able to respond to external perturbations, such as changing ground level, different ground properties as well as pushes and pulls at different body regions, in order to keep their balance and maintain an upright posture.

Given the current biomechanical understanding of human balance and posture control, it is still not well understood which neuro-muscular control mechanisms contribute to maintaining balance in response to external perturbations. In particular, it is not clear, how the contributions to recover from perturbations are organized at different levels, e.g. muscle mechanical response, spinal reflexes, and higher control contributions (e.g. from cortical areas in the brain). The present work focuses on improving this understanding by investigating human movement and posture control in response to different external perturbations. This thesis describes how healthy humans respond to unexpected external perturbations and identifies underlying neuro-muscular mechanisms enabling the motor system to cope with such challenges during locomotion and upright standing through passive and active strategies (e.g. tendon and muscles response, changed muscle activation).

The first part of the thesis presents previous research results in a systematic review thus providing insights into how leg function responds to external perturbations in selected motion tasks. It is shown that humans adjust their movements not only to the environmental context (e.g. when walking on even ground vs. slopes or climbing stairs) but also dependent on the state of their motion (i.e. current phase of gait, COM position) and in relation to the type of perturbation like changes in ground or external forces.

In the following part of the thesis, human standing experiments were designed to address the ability to cope with external perturbations with respect to axial and rotational leg function. Axial leg function described forces and displacements along the leg axis, pointing from the contact point of the foot to the COM. In contrast, rotational leg function described corresponding forces and displacements perpendicular to leg axis in sagittal plane. As predicted

by biomechanical leg models, the results show that biarticular muscles strongly contribute to the redirection of the GRF in order to maintain an upright posture.

In a second experimental study on human hopping, the ability to adapt leg stiffness (representing the axial leg function) in order to maintain cyclic movements in response to vertical ground level perturbations was investigated. The findings demonstrate a robust leg function, reflecting the ability of the human neuro-muscular system to cope with unexpected perturbations such as moving ground during hopping. An increase in leg stiffness was found in response to an upward surface acceleration.

This thesis describes and analyses the ability of the human body to respond to external perturbations leading to robust movement patterns. By translating the observed coping strategies into biomechanical and motor control models, new approaches for the design and control of legged systems (e.g. for assistive and rehabilitation devices) can be derived.

Zusammenfassung

Das posturale Gleichgewicht ist für die Kontrolle der menschlichen Körperhaltung sowohl im Stehen als auch bei zyklischen lokomotorischen Bewegungen wie Gehen und Laufen oder bei azyklischen Aufgaben wie der Ganginitiierung oder komplexen sportlichen Bewegungsabläufen entscheidend. Im Laufe der Evolution hat der Homo Sapiens eine aufrechte Haltung für die Zweibeinigkeit entwickelt und ermöglichte so den oberen Gliedmaßen (den Armen) die Interaktion mit Objekten. Die aufrechte menschliche Haltung ist gekennzeichnet durch zwei gestreckte Beine und einen Körperschwerpunk (KSP), welcher oberhalb der Hüfte liegt. Aufgrund der hohen KSP-Position wird die potentielle Energie maximiert und trägt zu einer größeren Manövrierfähigkeit im Hinblick auf eine schnellere Neuausrichtung der Körperachse und Bewegungsrichtung im Raum bei. Dennoch ist die Zweibeinigkeit im Vergleich zu anderen Morphologien, wie beispielsweise der vierbeinigen Körperkonfiguration bei Tieren, eine große Herausforderung. Die Zweibeinigkeit bietet zwar, wie erwähnt, viele Vorteile, erschwert aber auch Steuerungsfunktionen, insbesondere durch die Instabilität des biomechanischen Segment-Systems, welches wie eine sich aufrichtende Kette angeordnet ist. Um eine stabile aufrechte Haltung zu erreichen und ein Zusammenbrechen zu verhindern, ist es von grundlegender Bedeutung, alle Segmente oberhalb der Füße kontinuierlich auszubalancieren, indem geeignete Gelenkmomente aufgebracht werden und so die Ausrichtung der Bodenreaktionskräfte (GRF) fortwährend angepasst wird. Gleichwohl verleiht die Steuerung der menschlichen Motorik bei Aufgaben wie Stehen und Gehen Stabilität, auch gegenüber Störeinflüssen von außen. So kann der Mensch beim Auftreten dieser Störungen wie zum Beispiel wechselnden Bodenverhältnissen, unterschiedlichen Bodeneigenschaften sowie Stößen und Zugkräften an verschiedenen Körperregionen umgehen, um sein Gleichgewicht und somit eine aufrechte Körperhaltung zu bewahren.

Mit Blick auf das biomechanische Verständnis des menschlichen Gleichgewichts und der Haltungskontrolle ist aktuell noch nicht vollständig geklärt, welche neuro-muskulären Kontrollmechanismen dazu beitragen, das Gleichgewicht als Reaktion auf externe Störungen aufrechtzuerhalten. Insbesondere ist noch nicht vollständig erforscht, wie die Beiträge zur Kompensation von Störungen auf verschiedenen Ebenen der Muskelreaktion, spinaler Reflexe und der übergeordneten Kontrollsysteme wie zum Beispiel von kortikalen Bereichen im Gehirn organisiert sind. Die vorliegende Arbeit konzentriert sich darauf dieses Verständnis durch die Untersuchung der menschlichen Bewegungs- und Haltungskontrolle in Reaktion auf verschiedene äußere Störeinflüsse zu verbessern. Diese Dissertation beschreibt, wie gesunde Menschen auf unerwartete äußere Störungen reagieren und identifiziert dabei die zugrundeliegenden neuro-muskulären Mechanismen, die es dem Bewegungsapparat ermöglichen, mit solchen Herausforderungen während der Fortbewegung durch passive und aktive Strategien (z.B. Sehnen- und Muskelreaktion, veränderte Muskelaktivierung) umzugehen.

Im ersten Teil der Thesis stellt ein systematisches Review bisherige Forschungsergebnisse zusammen und gibt so Einblicke, wie die Beinfunktion auf externe Störungen in ausgewählten Bewegungsaufgaben reagiert. Es wird aufgezeigt, dass der Mensch seine Bewegungen nicht nur an den Umgebungskontext anpasst (zum Beispiel beim Gehen auf ebenem Untergrund gegenüber Anstiegen oder beim Treppensteigen), sondern auch an den aktuellen

Bewegungskontext (zum Beispiel momentane Gangphase, KSP-Position) sowie an die Art der Störung (zum Beispiel Bodenveränderungen oder externe Krafteinflüsse).

Im anschließenden Teil der Arbeit werden am Menschen durchgeführte Standexperimente vorgestellt, welche die Fähigkeit untersuchen, mit externen Störungen in Bezug auf die axiale und rotatorische Beinfunktion umzugehen. Die axiale Beinfunktion beschreibt hierbei Kräfte und Bewegungen entlang der Beinachse; die virtuelle Achse zeigt vom Kraftangriffspunkt des Fußes (am Boden) zum KSP. Im Gegensatz dazu beschreibt die rotatorische Beinfunktion entsprechende Kräfte und Verschiebungen orthogonal zur Beinachse in sagittaler Ebene. Wie von biomechanischen Beinmodellen vorhergesagt, bestätigen die Ergebnisse, dass zweigelenkige Muskeln stark zur Neuausrichtung der GRF beitragen und damit die aufrechte Körperhaltung unterstützen.

In einer zweiten experimentellen Studie, zum Hüpfen auf der Stelle, wird die Anpassungsfähigkeit der Beinsteifigkeit, die die axiale Beinfunktion widerspiegelt, bei vertikalen Bodenstörungen einen gleichmäßigen Bewegungsablauf aufrechtzuerhalten untersucht. Die Ergebnisse zeigen eine robuste Beinfunktion, die die Fähigkeit des menschlichen neuromuskulären Systems widerspiegelt, unerwartete Störungen (zum Beispiel das Nachgeben des Bodens) zu kompensieren. Darüber hinaus deuten die Erkenntnisse auf eine störungsabhängige Zunahme der Beinsteifigkeit (zum Beispiel durch Reflexe) als Reaktion auf eine Aufwärtsbeschleunigung des Untergrundes hin.

Diese Dissertation beschreibt und analysiert die Fähigkeit des menschlichen Körpers auf externe Störungen zu reagieren, die zu robusten Bewegungsmustern beiträgt. Die Übertragung der beobachteten Kompensationsstrategien auf biomechanische und motorische Kontrollmodelle ermöglicht neue Ansätze für das Design und die Kontrolle von (künstlichen) Bewegungssystemen wie zum Beispiel für Assistenz- und Rehabilitationsgeräte.

Contents

Acknowledgements

This dissertation[1] was written as part of my work as a scientific assistant at the Department of Sports Science at the Technische Universität Darmstadt. I would like to thank my PhD supervisor, Prof. Dr. André Seyfarth, who made this work possible. Andre promoted my professional understanding with valuable suggestions, inspiring discussions and advice; and moreover, gave me the opportunity to follow my ideas. And I would like to thank Prof. Dr. David Lee for taking over the second opinion.

My deepest thanks go to my girlfriend Bärbel, who has constantly supported and motivated me. For her great understanding and for the fact that she always stood behind me and strengthened me in my decisions. Tons of thanks go out to countless others who offered encouragement, direction, inspiration, instruction, or life-support. My family, friends, and colleagues, you know who you are; I won't mention any names.

[1] Supported by the B.A.L.A.N.C.E. – project (Balance Augmentation in Locomotion, through Anticipative, Natural and Cooperative control of Exoskeletons), which is partially funded under grant 601003 of the Seventh Framework Program (FP7) of the European Commission (Information and Communication Technologies, ICT-2011.2.1).

1. Introduction

It is fascinating watching athletes displaying high-level performances in their discipline. Working in the area of sports biomechanics, I am interested in investigating why they have achieved such a high level. From that my main question is: how do movements work? Athletes engaged in parkour execute such highly demanding movements as flips, twists and jumps from great heights including interactions with obstacles. In my opinion, the main challenge in parkour is not just performing these movements but sequencing them while running across rough terrain, including changing environmental conditions, without accidents which this would potentially lead to severe injuries. Therefore, athletes must have full control over their balance and motion execution at every moment. Slacklining is a no less demanding activity, but more focused on balancing meaning that practitioners must keep their balance on a very tight and above all unsteady line.

Other examples that are more oriented towards everyday life are walking very slowly and maintaining an upright stance (e.g. while manipulating objects or on difficult surfaces). The 2016 DARPA (Defense Advanced Research Projects Agency) challenge showed that most humanoid robots already failed to execute these simple tasks even before resolving the *real* challenges (Ackermann & Guizzo, 2015). In the course of evolution, Homo sapiens developed an upright posture for bipedalism, thus freeing the remaining limbs (arms) to interact with objects. Human upright stance is characterized by two straight legs and the center of mass (COM) is located above the hip, thus maximizing potential energy (due to high COM position) enabling great maneuverability for fast re-orientation of the body axis and re-direction of movement direction in space. Nevertheless, bipedalism is mechanically much more challenging (e.g. regarding stability) compared to other body morphologies in legged animals such as a quadrupedal leg configuration. This evolutionary innovation does not only provide benefits (such as those mentioned above), but also makes control functions difficult, which might involve instability of the whole mechanical system with segments arranged like an upside-down chain. To achieve the stable upright human stance and to prevent collapse, it is fundamental to continuously balance all segments above the feet by introducing appropriate joint torques and continuously adjusting the orientation of the ground reaction forces (GRF). Nevertheless, human motor control during tasks such as standing and walking provides stability in the case of external perturbations. Thus, humans are able to respond to external perturbations, such as changing ground level, different ground properties as well as pushes and pulls at different body regions, in order to keep their balance and maintain an upright posture.

With respect to the introductory example and regarding walking as a more complex motion task than standing, bipedal walking would require even greater balancing skills. Toddlers learn to walk in a much shorter time compared to the time they need to learn to stand upright (Iosa, Fusco, Morone & Paolucci, 2014; Maus, Lipfert, Gross, Rummel & Seyfarth, 2010). Initially, their gait still lacks smoothness, symmetry and stability but it quickly improves over time. A few years ago, Saus (2014) posted a blog entry provokingly speculating that “walking is the process of controlled stumbling”.

Using sophisticated sensory technologies such as electromyography (EMG) or electroencephalography (EEG) researchers are able to quantify biomechanical parameters of human (loco-) motion on the neurological and muscular level, respectively. These insights help

to improve our understanding of how complex motions are generated. However, little is yet known about the underlying platform in which these parameters are embedded. This platform connects and controls these parameters and thus controls human motions. Efforts have been made to create a benchmarking scheme in order to establish a common approach for the assessment and research of bipedal locomotion (Torricelli et al., 2015).

More insights and improved understanding of the embedding platform or the human operating system could also help engineers in the development and control of (humanoid) bipedal robots and exoskeletons. Although technological progress enables us to process more and better data gathered from cross-linked sensors in a shorter time, present robots and exoskeletons are easily outperformed by humans in terms of simple motion tasks such as balancing and locomotion. This could be readily observed in DARPA's Robotic Challenge where all the robots fell at least once for different reasons such as software failures or bugs (Ackermann & Guizzo, 2015). Furthermore, healthy humans can cope with most environmental influences and external perturbations quite easily and are prevented from falling by underlying (programmed) balance mechanisms to counteract external perturbations.

1.1. Biomechanical understanding of human balance and posture control

From a physical point of view, *balance* (or postural equilibrium) is defined as the relation of the COM position (of an object) to its base of support (BOS); i.e. the line of gravity (from COM to the ground) must end up within the BOS (Horak, 1988; Pollock, Durward, Rowe & Paul, 2000; Winter, 1995; Winter, Patla & Frank, 1990). In this way, *stability* represents the ability of an object to resist an external force before it becomes unbalanced; which means "the greater the displacement of the line of gravity before an object becomes unbalanced the greater the stability of that object" (Horak, 1988; Pollock et al., 2000). Transferring these principles and relations to humans' balance while standing upright means that they have to cope with a relatively high COM over a small BOS (Dietz, 1992; Maki & McIlroy, 1997; Massion, 1994; Mergner, 2012; Pollock et al., 2000; Taube & Gollhofer, 2012; Winter, 1995). Sensory information (e.g. somatosensory, vestibular or visual) enables humans to sense pending losses of (human) stability and then use muscular activity to restore it (Horak, 1988; Massion, 1994; Pollock et al., 2000) and thus control the relationship between the line of gravity and the BOS (Maki & McIlroy, 1997; Pollock et al., 2000). This ability to control balance is termed *postural control* and is fundamental for the maintenance of postures and activities which have been classified as: i) the maintenance of a specified posture, such as sitting or standing, ii) voluntary movement, such as the movement between postures, and iii) the reaction to an external disturbance, such as a trip, slip, or push (Berg, Wood-Dauphine, Williams & Gayton, 1989; Horak, 2006a; King, Judge & Wolfson, 1994; Pollock et al., 2000). Thus, *balance* or *postural control* is defined as "the act of maintaining, achieving or restoring a state of balance during any posture or activity" (Pollock et al., 2000).

Performing tasks within the three classified activities (see above) means applying postural control strategies, and here we will focus on the first (i.e. maintenance of a specified posture). There are three types of postural control strategies: reactive (compensatory), predictive (anticipatory), and a combination of the two (Maki & McIlroy, 1997; Pollock et al., 2000). Predictive strategies might be voluntary movements or increases in muscle activity in response

to an anticipated disturbance, whereas reactive strategies follow an unexpected disturbance. Both strategies are characterized either by fixed-support responses, i.e. the line of gravity is moved within the BOS such as voluntary body sway in the ankle or hip (ankle strategy or hip strategy), or by change-in-support responses, i.e. the BOS is moved to intersect the line of gravity such as grasping a fixed object or taking a step (stepping strategy) (Duncan, Studenski, Chandler, Bloomfeld & LaPointe, 1990; Hof, 2007; Horak, 1988, 2006a; Horak & Nashner, 1986; Maki & McIlroy, 1997; Mihelj, Matjačić & Bajd, 2000; Mille et al., 2003; Pollock et al., 2000; Rietdyk, Patla, Winter, Ishac & Little, 1999). Another mechanism for maintaining balance is to counter-rotate segments around the COM (Hof, 2007), also observed in slacklining (Huber & Kleindl, 2010; Neumann & Vallery, n.d.; Paoletti & Mahadevan, 2012).

Although human postural control has been seen as an inherent ability (Horak, 1988; Nashner, 1982; Pollock et al., 2000), the underlying strategies rely on the assessment and control of many variables by the central nervous system (CNS) (Horak, Henry & Shumway-Cook, 1997; Pollock et al., 2000). In this way and due to the fact that toddlers first have to learn to balance their body before being able to walk (Adolph & Robinson, 2013), postural control may be seen as a fundamental motor skill that has to be learnt by the CNS and becomes more efficient and effective with training and practice (Horak et al., 1997; Pollock et al., 2000).

After providing a brief overview on what happens in human balance and when postural control strategies are applied, it is still open how humans implement postural control strategies. In the following, we will briefly introduce common conceptual models and control concepts that help to refine und improve the usual understanding of postural control strategies.

In engineering as well as in biology, there are similar approaches for characterizing the different postural control strategies: on the one hand, closed-loop models in engineering vs. feedback control in biology, and, on the other hand, open-loop models vs. feedforward control. In feedforward control (see Figure 1.1), rhythmic movements such as walking can be generated without the need for any sensory information (Enoka, 2002; Marder & Bucher, 2001). Potential disturbances are anticipated (or foreseen) and adequate counter-movements are initiated in good time (Taube & Gollhofer, 2012), e.g. to maintain posture or execute a movement. Therefore, it is necessary that the controller is aware of the state of the system and the required pathways to achieve the desired outcome (Enoka, 2002; Kawato, 1999). Changing the environmental conditions may disturb the execution of the movement; feedback is then needed to adjust the command signals in order to successfully perform the desired task (Enoka, 2002). Feedback control or closed-loop models (see Figure 1.1) work by comparing a desired state (i.e. task execution) and the actual state of the system by sensory information that is fed back to the controller (Enoka, 2002; van der Kooij, van Asseldonk & van der Helm, 2005). Depending on this difference, the system (human body) has to react by regulating the actual state (e.g. by increasing or decreasing muscle activity) to achieve the desired state.

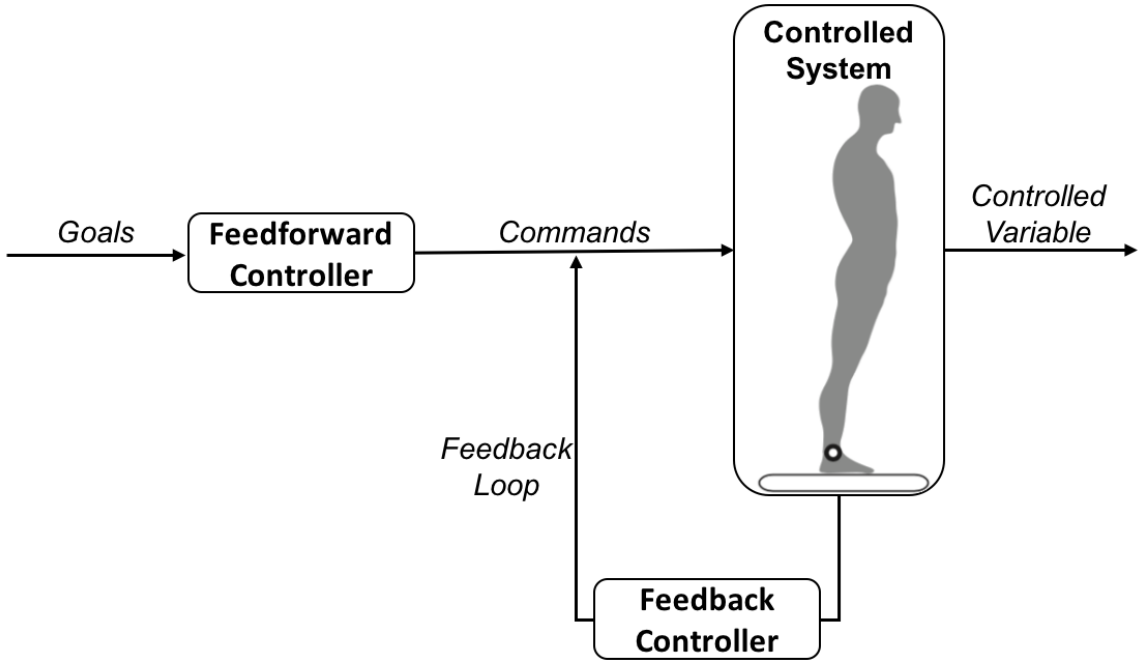


Figure 1.1: *Representation of feedforward and feedback control (modified from Enoka (2002); Mergner (2012)).*

In the human body, the sensory feedback information required for feedback control is retrieved from visual, vestibular and somatosensory systems; whereas the relative contribution of each system depends on the specific movement tasks and goals and the environmental context (Horak, 2006a). The proprioceptive systems consists of different receptors providing different types of sensory information: muscle spindles – muscle length and velocity of stretch and contraction; Golgi tendon organs – muscle force; and joint receptors – information about position, displacement, velocity and acceleration of movement (Enoka, 2002; Häufle, Grimmer, Kalveram & Seyfarth, 2012). Similar to visual and vestibular feedback, the information from the individual receptors must be processed by the CNS to generate the corresponding feedback. However, continuous re-weighting of the relative contributions is important to maintain stability, especially when the sensory context unexpectedly changes (Peterka, 2003). Hence, individuals with impaired sensory systems have a higher risk of falling (Horak, 2006a).

Reflexes initiate general motor programs triggered by sensory input (Zehr & Stein, 1999), e.g. sudden stretching of a muscle probably resulting from an external perturbation. Based on short-latency connections between input (afferent signal) and output (efferent signal), sensory receptors can initiate rapid responses (e.g. motor responses) that counteract the perturbation. The input-output connection is realized by neural circuits that perform a negative-feedback function which means counteracting the stimulus that initially activated the sensory receptor (Enoka, 2002). Enoka (2002) describes reflexes as follows:

> The simplest neural circuit underlying a reflex involves a sensory receptor and its afferent innervation, as well as a group of motor units that receive input from the afferent. This circuit, however, can be embedded in the neural elements controlling single muscle, can be distributed among a group of synergists …, can involve an interaction between an

agonist-antagonist pair of muscles, or can require the coordination of muscles in contralateral limbs.

The stretch reflex represents the response of a muscle to a brief, unexpected increase in length (a stretch) and supports the muscles in maintaining spring-like behavior (Enoka, 2002). Reflexes are characterized by two components: the short-latency response and the long-latency response. Both generate early reactions (preceding voluntary motor control) in muscle activity (EMG signals), whereas short latency response is about 30 ms and long latency response around 50 to 60 ms, the earliest voluntary motor control appears after 170 ms (Enoka, 2002). Similar to reflexes, automatic responses rely on feedback from sensory receptors, although their output behavior and neural control is more complex (Enoka, 2002). Humans continuously perform automatic responses such as motor control strategies to control small displacements of the COM to remain balanced and maintain an upright posture.

In general, it is possible to realize stable motion tasks such as standing, walking and running by feedforward (Ernst, Geyer & Blickhan, 2009; Seyfarth, Geyer, Günther & Blickhan, 2002; Seyfarth, Geyer & Herr, 2003) or feedback control (Alexandrov, Frolov, Horak, Carlson-Kuhta & Park, 2005; Fitzpatrick, Burke & Gandevia, 1996; Geyer, Seyfarth & Blickhan, 2003; Maurer & Peterka, 2005; Welch & Ting, 2008). In combination, the two control schemes can also complement each other, which leads to additional stability benefits (Dietz, Trippel, Ibrahim & Berger, 1993; Häufle et al., 2012; Müller, Häufle & Blickhan, 2014).

In the past few years, mechanical control concepts have been developed to improve the current understanding of complex postural control. Two equivalent concepts, the extrapolated center of mass (xCOM) and the capture point are used to estimate the state of balance (Vallery, Bögel, O´Brien & Riener, 2012) and provide space for foot placement that enables balance to be maintained or recovered during static and dynamic tasks. The xCOM considers the position of the vertical projection of the COM on the ground, its velocity plus a certain factor. As a result of the relation between the xCOM and the boundaries of the BOS, the margin of stability (MOS) serves as a measure of stability (Hof, Gazendam & Sinke, 2005). Considering hip or limb (arms and legs) motion, the xCOM may move outside of the BOS region during locomotion, although a balanced posture might still be restored (Hof et al., 2005). In this context and to realize stable walking “the [center of pressure] COP should be placed at a certain distance behind and outward of the xCOM at the time of foot contact” (Hof, 2008). The capture-point concept, which is often used in engineering and robotics, computes the region on the ground on which it is safe to step (e.g. to come to a complete halt). Therefore, “the intersection between the Capture Region and the Base of Support determines which strategy the robot should adopt to successfully stop in a given situation“ (Pratt, Carff, Drakunov & Goswami, 2006).

In order to realize posture control during standing and walking, humans (and animals) create a virtual pivot point (VPP) above the actual COM which is sufficient to achieve and maintain postural stability during a variety of tasks such as walking and running (Maus et al., 2010) as well as hopping (Sharbafi et al., 2012; Sharbafi, Maufroy, Ahmadabadi, Yazdanpanah & Seyfarth, 2013). Based on this virtual pendulum (VP) concept, other (neuromechanically inspired) concepts such as the force modulated compliant hip (FMCH) control, considering leg forces as sensory input for postural control in walking and running (Sharbafi & Seyfarth, 2014, 2015), have been developed.

1.2. Scope of the work & thesis outline

Given the current biomechanical understanding of human balance and posture control, it is still not well understood which neuro-muscular control mechanisms contribute to maintaining balance in response to external perturbations. In particular, it is not clear, how the contributions to recover from perturbations are organized at different levels, e.g. muscle response, spinal reflexes, and higher control contributions (e.g. from cortical areas in the brain). The present work focuses on improving this understanding by investigating human movement and posture control in response to different external perturbations. Therefore, three different studies have been conducted.

Chapter 2 aims to elucidate how humans respond to external perturbations and what coping strategies and mechanisms are applied to maintain balance. It also includes a systematic review of the relevant literature on these (specific) areas of research. Identified publications were analyzed in a perturbation matrix (PMA) composed of the selected motion tasks and types of perturbations. The PMA was used to highlight research areas and to suggest future research directions. Results in the highlighted research areas were reviewed to improve the understanding of human balance strategies, underlying balance mechanisms and motor control for coping with unexpected perturbations. Furthermore, the PMA was taken into account for the development of research questions in this thesis.

A conceptual model with appropriate segment length (1:1 thigh to shank length ratio) and moment arm ratios of two-joint muscles (2:1 for hip vs. knee, and for ankle vs. knee) demonstrates the decoupling of postural control (via biarticular muscles) from axial leg force production (via monoarticular muscles) (Rode & Seyfarth, 2013). In this way, humans may be able to manipulate leg forces perpendicular to the leg axis (this refers to the rotational leg function) by activating biarticular leg muscles. Following this approach, the response of human leg function (mono- and biarticular leg muscles) to quasi-static horizontal perturbations (pulls at shoulder and ankle level) while standing upright is investigated in Chapter 3.

Chapter 4 deals with neuro-muscular control mechanisms, i.e. adjustments of leg behavior (e.g. leg stiffness and leg impedance), in response to sudden changes of ground level during hopping on the spot.

The overall goal of this thesis is to describe how healthy humans respond to unexpected external perturbations and to identify neuro-muscular mechanisms enabling the motor system to cope with unexpected perturbations during locomotion through mechanical responses (e.g. tendon elasticity) and motor control (e.g. muscle activation).

2. Balance recovery in response to external perturbations during daily activities – a systematic review.

Author contributions

Dario Tokur is the main author of this chapter. He was responsible for the conception, literature research and analysis of relevant publications and writing of the texts. Martin Grimmer contributed to the introduction. Andre Seyfarth contributed to develop the research concept and revision of this chapter. This chapter was submitted in similar form to the Journal of Human Movement Science in January 2018 (current state: under review)[2].

2.1. Introduction

Human locomotion is an apparently easy task, but as yet the mechanics and control of locomotion are not fully understood. As already outlined in Chapter 1, once children have learnt to balance their bodies, they soon start to walk (Adolph & Robinson, 2013) and over time they manage to execute most daily activities without concentrating on the specific task. Balance is critical for posture control when standing upright and during cyclic tasks such as walking or running, as well as acyclic tasks such as gait initiation or complex sport movements.

Balance (or posture control) is defined differently depending on the specific motion task. *Balance* in static situations such as standing requires the vertical projection of the body center of mass (COM) so that it remains within the base of support (BOS) with minimal movement (Hof et al., 2005; Horak, 1988; Winter, 1995; Winter, Patla & Frank, 1990). The BOS describes the possible range of the center of pressure (COP) (Hof et al., 2005). During locomotion tasks, the term balance often implies robust and safe task execution known as *dynamic balance* (Winter, 1995). In other words, dynamic balance leads to stable position and posture control while the task is being performed (Bressel, Yonker, Kras & Heath, 2007; Winter et al., 1990). Hof et al. (2005) proposed to determine the margin of stability (MOS) which measures dynamic stability by using the extrapolated center of mass position (xCOM) relative to the BOS or the COP position. The xCOM is described by:

$$u - x = -\frac{l}{g}\ddot{x} = -\frac{\ddot{x}}{\omega_0^2} \text{ [E1]},$$

with x being the vertical projection of the COM, u the COP position, l leg length, g gravitational acceleration, and $\omega_0 = \sqrt{g/l}$ a new parameter (Hof et al., 2005). In this way, the relation (i.e. the minimal distance) between xCOM and the boundaries of the BOS defines the MOS (Hof et al., 2005). Considering hip or limb motions, the xCOM may move outside of the BOS region during locomotion, but a balanced posture may nevertheless be restored (Hof et al., 2005).

Up to the age of about 70 years (UK Department for Transport, 2014), approximately 20 % of all daily activities in adults involve walking. Healthy persons (with moderate physical activity

[2] Tokur, D.; Grimmer, M. & Seyfarth, A. (2017). Balance recovery in response to external perturbations during daily activities - a systematic review. *Human Movement Science*. Manuscript submitted for publication.

in their job) walk about 6500 steps per day (Tudor-Locke & Bassett, 2012). However, in the elderly functional limitations decrease walking distance (Hall & McAuley, 2010) and 57 % of falls during walking are due to stumbling, tripping and slipping (Do, Breniere & Brenguier, 1982; Schiller, Kramarow & Dey, 2007). Do, Chang, Kuran and Thompson (2015) showed that 73 % of fall-related injuries among Canadian seniors occur during walking: 16 % of falls happen during walking on snow or ice, 12 % during stair walking, and 45 % while walking on surfaces other than snow or ice. Other reasons for fall-related injuries include health problems (7 %), interacting with furniture or rising from furniture (6 %), physical activity (5 %), and elevated positioning (4 %) (Do et al., 2015). An overview of the distribution of daily activities (A) and reasons for falls (B) is provided in Figure 2.1

Patients with reduced balance ability may also experience difficulty in executing daily activities, especially those involving complex motion tasks. Dual tasks and external influences can further increase the level of difficulty (Springer et al., 2006). In the elderly, deficits in proprioception affect sensorimotor tasks such as balancing (Goble, Coxon, Wenderoth, Van Impe & Swinnen, 2009). Moreover, reduced muscle force, contraction velocity and power influence human balance and posture (Maki & McIlroy, 2006). Consequently, the number of falls in adults increases with age (Rubenstein & Josephson, 2002). Talbot, Musiol, Witham and Metter (2005) investigated that 34.8 % of the elderly (mean age, 76.2 years) compared to 18.5 % of adults (mean age, 35.3 years) reported falling at least once in two years. In addition, 30 to 50 % of elderly fallers incur injuries requiring medical attention or limiting their daily activities for at least one day (Hong, Cho & Tak, 2010; Stevens, Mack, Paulozzi & Ballesteros, 2008). Reasons for loss of balance may be classified into two categories: internal factors such as diseases and disorders (Healthline Networks, Inc., 2015; Mayo Clinic, 2015; National Institute on Deafness and Other Communication, 2015; Vestibular Disorders Association, 2015; Wikipedia, 2015), and external factors such as uneven or slippery ground, or unexpected perturbations (Hof, Vermerris & Gjaltema, 2010; Marigold & Patla, 2002; Voloshina, Kuo, Daley & Ferris, 2013).

The number of steps taken per day decreases with age whereas the rate of injuries, hospitalization rate and fall-related deaths during daily activities increase with age (Do et al., 2015; Stinchcombe, Kuran & Powell, 2014), so that improving gait stability and balance would presumably improve the quality of life in the elderly population.

Compared to impaired and elderly people, healthy young persons can tolerate larger perturbations before they fall (Maki & McIlroy, 2006). This does not imply smaller or weaker disturbances but rather the more effective use of balancing and coping mechanisms, e.g. feedback control (Alexandrov et al., 2005; Häufle et al., 2012) or changes of leg parameters (Riese & Seyfarth, 2011) and balance strategies (e.g. systematic changes in the gait pattern or modulation of joint torques (Hof, 2009). Stergiou and Decker (2011) reviewed and evaluated concepts of variability and concluded that variability in the execution of movements is beneficial for coping with external perturbations.

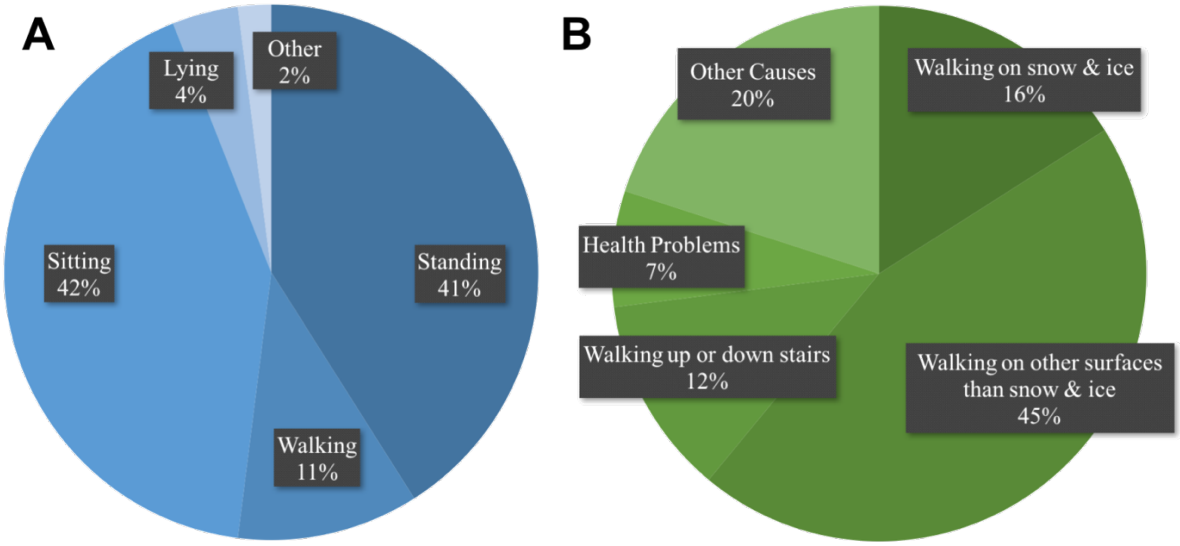


Figure 2.1: *(A) Relative time spent on different motion tasks among retired people with a mean age of 66 years within 12 hours after waking (modified from (Pitta et al., 2005). (B) Causes of falls among persons over 65 years (modified from (Do et al., 2015).*

A better understanding of human motor control and coping mechanisms and strategies may help to improve the quality of life for persons with disorders or disabilities. This knowledge would be useful in the development of assistive devices that support daily tasks or physical activities and improve mobility and health. The aim of this study was to examine how humans respond to external perturbations and what coping mechanisms and strategies are applied to maintain or restore balance and to prevent falling, and also to review the literature on these (specific) areas of research. We reviewed relevant publications and summarized findings to gain a broader understanding of coping mechanisms and strategies, including movement responses to specific external perturbations, and to identify gaps in the literature that require further research.

Table 2.1: *List of introduced abbreviations in Chapter 2.*

Abbreviation	*Definition*
BOS	Base of support
COM	Body center of mass
COP	Center of pressure
EMG	Electromyography
GRF	Ground reaction forces
MOS	Margin of stability
PMA	Perturbation matrix
xCOM	Extrapolated center of mass
AP	Antero-posterior
ML	Medio-lateral
V	Vertical
GM	Gastrocnemius muscle
BF	Biceps femoris muscle
TA	Tibialis anterior muscle
SL	Soleus muscle
RF	Rectus femoris muscle

2.2. Method

We conducted a systematic review of the literature to identify relevant publications. We first identified relevant motion tasks and perturbations; next we defined the inclusion and exclusion criteria; then we searched for appropriate literature and academic publications; and we finally extracted findings from the selected publications.

2.2.1. Motion tasks and perturbations

Besides the common motion tasks of daily activities, standing and walking (see Figure 2.1), we selected running and hopping, which represent highly dynamic types of locomotion. Similar to previous studies (Do et al., 2015; Schiller et al., 2007), we chose several external perturbations: **external forces** (e.g. pushes and pulls); **ground changes** (such as sudden elevations and drops, property changes, or ground movements); and **obstacles** (see Table 2.3 and Table 2.4). Internal perturbations such as joint torque manipulation (e.g. from instrumented orthoses) and others were excluded from this review. Figure 2.2 illustrates the selected perturbations for the example of walking.

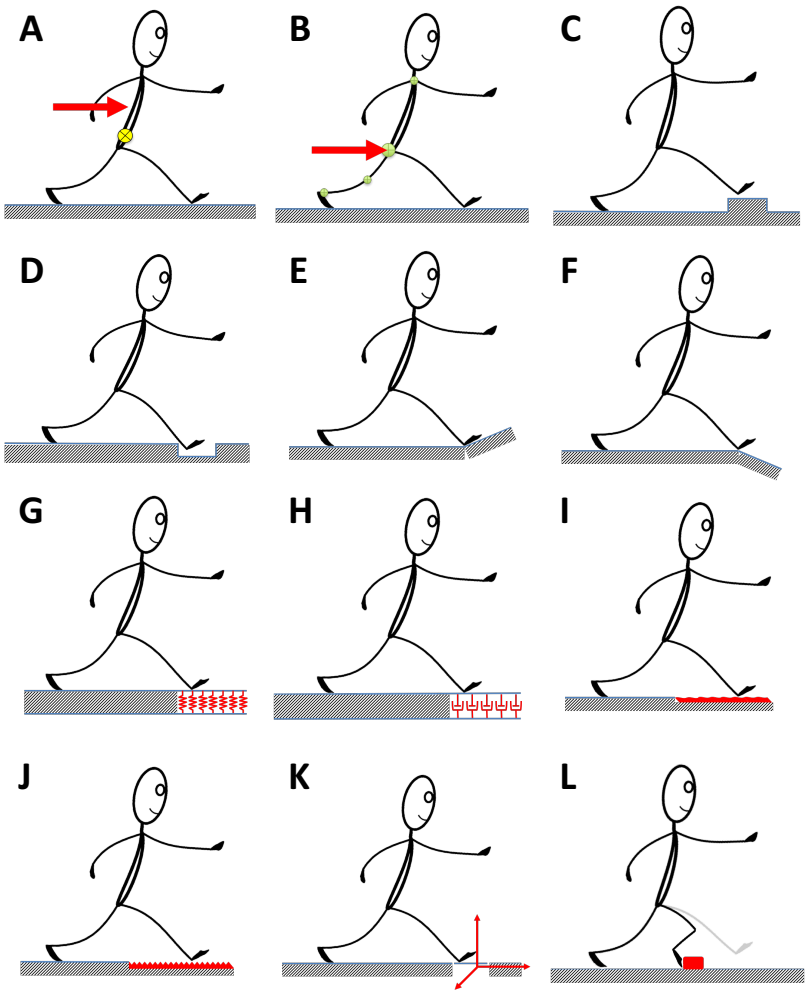


Figure 2.2: *External perturbations in walking. A+B: red arrows indicate external forces applied to body regions and COM (A) or joints (B). C+D: changes in ground level height upwards (C) or downwards (D). E+F: transition to an upward (E) or downward slope (F), respectively, walking on these slopes. G-J: altered ground properties such as elastic (G), dampened (H), slippery (I) or non-slippery surfaces (J). K: red arrows indicate movements of the ground (x-, y- and z-direction). L: obstacles (e.g. blocking of the swing leg).*

2.2.2. Inclusion and exclusion criteria

In general, we considered publications that studied responses to perturbations and identified compensation mechanisms. To limit the number of publications, we included or excluded manuscripts based on the following criteria given in Table 2.2.

Table 2.2: *List of criteria for inclusion or exclusion of literature.*

Inclusion criteria	*Exclusion criteria*
Experiments	
• Healthy adults • External mechanical perturbations • Selected motion tasks • Biomechanical measurements, including kinetics, kinematics, muscle activity recordings	• Patients or disabled people • Animals • Internal perturbations (proprioceptive, vestibular, neuronal) • Visual perturbations (eyes closed, moving surroundings) • Comparisons (gender, age, training, etc.)
Simulation models	
• Biomechanical simulation models (inverse dynamics, feedforward models) • Different levels of model complexity from simple to detailed models (e.g. OpenSim, AnyBody)	• Control strategies (e.g. feedback models)

2.2.3. Literature search

The literature was searched using online search engines (*Google Scholar*) considering different combinations of keywords relevant for the research question: external, perturbations, disturbances, human, standing, walking, running, hopping, vertical, horizontal (last search date, May 2015).

In this review, we considered publications that matched all the inclusion criteria (see Section 2.2.2). Publications were rejected if they met any exclusion criterion. Individual exceptions were made, for instance for papers that studied both healthy and clinical populations, but in this case relevant findings for healthy subjects were considered separately from clinical subjects.

Relevant publications were added to our perturbation matrix (PMA). The PMA (Table 2.3 and Table 2.4) consists of two dimensions: different motion tasks (standing, walking, running, hopping) and different external perturbations (e.g. surface translations, pushes or pulls, inclines, ground level changes; see Figure 2.2). The publications were clustered according to the PMA categories.

2.3. Results and discussion

2.3.1. The perturbation matrix

By evaluating the PMA (Table 2.3 and Table 2.4), we identify well-covered and less well-covered areas of research (described by motion tasks and type of external perturbation). We highlight areas of research with at least five assigned publications (see Table 2.3 and Table 2.4, dark green cells). These areas of research are further discussed in this review.

2.3.2. Responses to perturbations while standing

In this section, we present findings and insights from the systematic review of the motion task of standing and, in particular, the perturbation types of *external forces* and *moving ground*.

External forces (joints, body regions, COM)

External forces acting on the body during standing challenge balance and require corrective actions to maintain or restore body posture.

Among other strategies, reflex ankle stiffness enables balance to be maintained and ensures that small perturbations can be coped with (Fitzpatrick, Taylor & McCloskey, 1992). These authors suggest that the muscle-reflex system generates adequate ankle stiffness (calculated as the relation of ankle torque and ankle angle) to facilitate an upright posture. The muscle-reflex system provides a base postural stability that is fine-tuned by visual and vestibular reflexes (Fitzpatrick et al., 1992). The effective manipulation of muscle-reflex stiffness results in changes of ankle moments and is termed the *ankle strategy* (Horak & Nashner, 1986; Mihelj et al., 2000; Rietdyk et al., 1999). With sufficient ankle stiffness, the inverted pendulum of the upright human body (Gage, Winter, Frank & Adkin, 2004; Kalmus, 1970; Winter, 1995) can be transformed into a virtual pendulum model, similar to the virtual pivot point concept introduced at the hip level (Maus et al., 2010). However, to date it is still unclear whether the neural control circuits at the ankle and hip levels are similar.

To study the responses of the ankle and hip to perturbations in order to restore posture during standing, Mihelj et al. (2000) investigated the influence of different initial lean angles on balance recovery for different perturbation types (i.e. combinations of torque and duration) with constrained knees (i.e. limited knee flexion). The results indicated that the reaction to **anterior perturbations** at the hip level comprises a mechanical response (trunk extension due to the perturbation) and an active response (hip flexion with concomitant trunk flexion to restore initial posture), and the ankle angle decreased (Mihelj et al., 2000). In contrast, in reaction to **posterior perturbations**, the ankle angle increased and the trunk angle (trunk extension) decreased. Timing and magnitude of these compensation mechanisms differ according to perturbation type: while the hip angle only changed in magnitude for anterior perturbations, (almost linearly), the hip angle changed in timing and magnitude for posterior perturbations, and the ankle showed similar behavior (Mihelj et al., 2000).

Table 2.3: *The PMA for the motion tasks of standing and walking. Dark green – areas of research with at least five publications; light green – areas of research with less than five publications; red - no publications; crossed out - areas of research not considered at all. ML: medio-lateral direction; AP: anterior-posterior direction; V: vertical direction; EXP: experimental studies; MOD: modeling and simulation studies.*

Perturbation		**Motion Task**	
Type	***Feature***	***Standing***	***Walking***
External forces *(region, joints, COM)*		**EXP** (Fitzpatrick et al., 1992; Mille et al., 2003; Blickhan, Ernst, Koch & Müller, 2013; Fitzpatrick et al., 1996; Rietdyk et al., 1999; Mihelj et al., 2000; Kudoh, Komura & Ikeuchi, 2004) **MOD** (Kudoh, Komura & Ikeuchi, 2002; Kudoh et al., 2004)	**EXP** (Bachmann, Müller, van Hedel & Dietz, 2008; Dietz, Quintern, Boos & Berger, 1986; Hof & Duysens, 2013; Hof et al., 2010; IJmker, Lamoth, Houdijk, van der Woude & Beek, 2014; Yang, Winter & Wells, 1990) **MOD** (Yang et al., 1990)
Ground changes	**Ground level** *(up, down)*		**EXP** (Andriacchi, Andersson, Fermier, Stern & Galante, 1980; McFadyen & Winter, 1988; Müller, Tschiesche & Blickhan, 2014; Nadeau, McFadyen & Malouin, 2003; Protopapadaki, Drechsler, Cramp, Coutts & Scott, 2007; Riener, Rabuffetti & Frigo, 2002; van der Linden, Marigold, Gabreëls & Duysens, 2007; van Dieën, Spanjaard, Konemann, Bron & Pijnappels, 2007; van Dieën, Spanjaard, Könemann, Bron & Pijnappels, 2008; Voloshina et al., 2013) **MOD** (Rummel, Blum & Seyfarth, 2010)
	Slopes *(up, down)*	**EXP** (Carpenter, Allum & Honegger, 1999; Leroux, Fung, & Barbeau, 2002; Nardone, Giordano, Corrà & Schieppati, 1990; Nashner, Woollacott & Tuma, 1979)	**EXP** (Hansen, Childress & Miff, 2004; Kawamura, Tokuhiro & Takechi, 1991; Kuster, Sakurai & Wood, 1995; Lay, Hass & Gregor, 2006; Leroux, Fung & Barbeau, 1999; McIntosh, Beatty, Dwan & Vickers, 2006; Nashner, 1980; Prentice, Hasler, Groves & Frank, 2004; Redfern & DiPasquale, 1997; Sun, Walters, Svensson & Lloyd, 1996)
	Slopes *(ML)*	**EXP** (Carpenter et al., 1999)	*(no publications)*

Perturbation		Motion Task	
Type	***Feature***	***Standing***	***Walking***
	Ground properties *(elastic, damped)*	*(no publications)*	**EXP** (Lejeune, Willems & Heglund, 1998; Marigold & Patla, 2005)
	Structure *(friction)*	*(no publications)*	**EXP** (Cappellini, Ivanenko, Dominici, Poppele & Lacquaniti, 2010; Marigold & Patla, 2002) **MOD** (Pai & Iqbal, 1999; Yang, Anderson & Pai, 2008)
	Moving *(AP, ML)*	**EXP** (Burleigh, Horak & Malouin, 1994; Henry, Fung & Horak, 1996, 1998a, 1998b, 2001; Maki & McIlroy, 1999; McIlroy & Maki, 1999; Nardone et al., 1990; Nashner et al., 1979; Runge, Shupert, Horak & Zajac, 1999) **MOD** (Maki & McIlroy, 1999)	**EXP** (Brady, Peters & Bloomberg, 2009; Ferber, Osternig, Woollacott, Wasielewski & Lee, 2002; Hak et al., 2013; Nashner, 1980; Oddsson, Wall, McPartland, Krebs & Tucker, 2004; Sari & Griffin, 2014; Tang, Woollacott & Chong, 1998; Yang & Pai, 2010)
	Moving *(V)*	**EXP** (Nashner et al., 1979)	**EXP** (Klint, Nielsen, Sinkjaer & Grey, 2009; Nashner, 1980)
	Obstacles		**EXP** (Cordero, Koopman & van der Helm, 2004; Eng, Winter & Patla, 1994; Grabiner, Koh, Lundin & Jahnigen, 1993; Pijnappels, Bobbert & van Dieën, 2005; Schillings, Van Wezel & Duysens, 1996; Schillings, van Wezel, Mulder & Duysens, 2000) **MOD** (Cordero, Koopman & van der Helm, 2003; Cordero et al., 2004; de Boer, Wisse & van der Helm, 2010; Yamasaki, Nomura & Sato, 2003)

Table 2.4: *The PMA for the motion tasks of running and hopping. Dark green – areas of research with at least five publications; light green – areas of research with less than five publications; red – no publications; crossed out – areas of research not considered at all. ML: medio-lateral direction; AP: anterior-posterior direction; V: vertical direction; EXP: experimental studies; MOD: modeling and simulation studies.*

Perturbation		**Motion Task**	
Type	***Feature***	***Running***	***Hopping***
External forces *(region, joints, COM)*		(no publications)	**MOD** (Sharbafi & Seyfarth, 2013)
Ground changes	**Ground level** *(up, down)*	**EXP** (Ernst, Götze, Müller & Blickhan, 2014; Grimmer, Ernst, Günther & Blickhan, 2008; Müller & Blickhan, 2010; Müller, Grimmer & Blickhan, 2010; Müller, Ernst & Blickhan, 2012; Müller, Häufle, et al., 2014; Voloshina & Ferris, 2015) **MOD** (Ernst et al., 2009; Müller, Häufle, et al., 2014; Rummel & Seyfarth, 2008; Seyfarth et al., 2003)	(no publications)
	Slopes *(up, down)*	**EXP** (Kuster et al., 1995)	**EXP & MOD** (Kalveram, Häufle, Seyfarth & Grimmer, 2012)
	Slopes *(ML)*	(no publications)	(no publications)
	Ground properties (elastic, damped)	**EXP** (Alcaraz, Palao, Elvira & Linthorne, 2011; Ferris, Liang & Farley, 1999; Ferris, Louie & Farley, 1998; Hardin, Van Den Bogert & Hamill, 2004; Kerdok, Biewener, McMahon, Weyand & Herr, 2002; Lejeune et al., 1998; Pinnington, Lloyd, Besier & Dawson, 2005) **MOD** (Ferris et al., 1999; Hurst, Morris, Chestnutt & Rizzi, 2007)	**EXP** (Farley, Houdijk, Strien & Louie, 1998; Ferris & Farley, 1997; Moritz & Farley, 2003, 2005) **MOD** (Farley et al., 1998; Moritz & Farley, 2003, 2004; van der Krogt et al., 2009)
	Structure *(friction)*	(no publications)	(no publications)
	Moving *(AP, ML, V)*	(no publications)	(no publications)
	Obstacles	(no publications)	

To counteract the greater body sway caused by the perturbation (either in the anterior or posterior direction), measured ankle torques oppose the change in the ankle angle (Mihelj et al., 2000). Whilst the ankle torque amplitude changed for the different perturbation types, ankle torques changed less for posterior than for anterior perturbations (Mihelj et al., 2000). The specific asymmetries in the changes at the ankle and hip in response to perturbation direction may be due to asymmetric foot geometry since the potential to produce counteracting torques at the ankle is smaller for backward than for forward sway.

Pushes applied to the trunk and pelvis in the medio-lateral (ML) direction elicit joint-specific torque changes controlling the COP position to keep the COM within the BOS and hence control the lateral excursion of the trunk (Rietdyk et al., 1999). In this context, the contributions of the joints to balance recovery were experimentally quantified: in the frontal plane the response was dominated by hip and spinal torques (85 %) in comparison to ankle torques (15 %) (Rietdyk et al., 1999).

In standing, humans additionally use the hip strategy (i.e. changes in hip moments due to hip motion (Horak & Nashner, 1986)) if the ankle strategy is insufficient to maintain an erect posture in response to external perturbations (Rietdyk et al., 1999; Mihelj et al., 2000). Further strategies of push compensation were identified by Kudoh et al. (2002, 2004) using a computer simulation model of the segmented human body. They identified three strategies used to maintain balance in the case of large perturbations: rotating the arms, bending the trunk downwards, and taking a step. The first two strategies control the angular momentum while remaining standing (Kudoh et al., 2002). For larger perturbations, taking a step is required to augment angular momentum control (Kudoh et al., 2004). Similarly, Mille et al. (2003) investigated the limits of balance control in stance and suggested a threshold boundary (defined by pelvis position in relation to the BOS, measured from the axis of the ankles) between the joint strategy (i.e. angular momentum control in stance) and the need to take a step to prevent falling. Irrespective of perturbation speed, a step must be taken to avoid falling once the threshold boundary is crossed. However, this threshold boundary shifts closer to the ankle with increased perturbation speed (Mille et al., 2003).

Moving ground

In this section, we address studies in which subjects experience sudden translations of the supporting ground in the anterior-posterior (AP) and medio-lateral (ML) direction while standing still.

Early responses to ground translations were observed in the activation of the gastrocnemius (GM) and soleus (SL) muscles indicating usage of the ankle strategy (Burleigh et al., 1994; Nardone et al., 1990). In response to **backward translations** of the ground during standing, electromyography (EMG) and joint kinematics as well as resulting joint torques indicate application of the ankle strategy (Burleigh et al., 1994; Runge et al., 1999) with additional use of the hip strategy for greater postural displacements (Runge et al., 1999). Similar usage of the ankle and hip strategy has already been described in the section on external forces while standing.

Kinematic responses to restore the erect posture after **AP** and **ML ground movements** similarly display a sequential displacement and recovery (return to the original condition) of the shank, thigh and trunk segments with distal-to-proximal progression in order (Henry et al., 1998a). While the recruitment of leg muscles shows a distal-to-proximal cascade, the trunk and hip muscles are recruited earlier or at the same time (Henry et al., 1998a).

Muscle synergies (i.e. simultaneous activation of muscle groups) control equilibrium in stance but depend on the perturbation direction (Henry et al., 1998b).

Figure 2.3 shows the perturbation direction (A) and corresponding polar plots of the muscle activation curves in relation to the perturbation direction (B – D). Similar activation of the leg muscles was found in other studies (Nardone et al., 1990; Nashner et al., 1979). In the experimental setup by Henry et al. (1996, 1998a), ground reaction forces (GRF) showed a two-stage response pattern: a passive short-time response (50 – 100 ms) with GRF pointing opposite to the perturbation direction, and a subsequent active response (100 – 300 ms) with restoring forces that create the necessary torques around the body COM to realign the body orientation. This effect was more pronounced in ML perturbations (Burleigh et al., 1994; Henry et al., 1996, 1998a) indicating that lateral perturbations may lead to larger postural misalignments than AP perturbations. This phenomenon may be due to the asymmetric foot geometry and the lateral load shift from one leg to the other with strong implications for the underlying motor control strategies and may also be relevant for other motion tasks (e.g. walking, discussed in the next section).

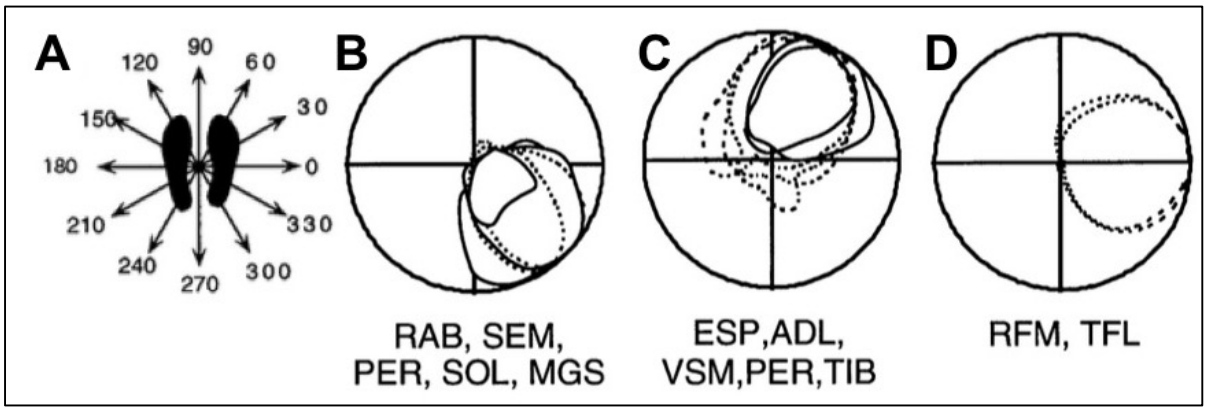


Figure 2.3: *Perturbation-dependent muscle synergies in stance. A: the 12 perturbation directions. B: perturbation-direction-dependent activity of muscle groups averaged over five trials. Muscles: tibialis anterior (TIB), peroneus longus (PER), medial gastrocnemius (MGS), soleus (SOL), vastus medialis (VSM), rectus femoris (RFM), adductor longus (ADL), semimembranosus (SEM), tensor fascia latae (TFL), rectus abdominis (RAB) and erector spinae (ESP) – adapted from (Henry et al., 1998b).*

2.3.3. Responses to perturbations while walking

In this section, we review balance maintenance during walking. With respect to the PMA (Table 2.3), we report on responses to perturbations including *external forces*, *ground level changes, slopes, moving ground* as well as *obstacles*.

External forces (joints, body regions, COM)

Balance maintenance during walking and the specific recovery strategies strongly depend on the type of perturbation (specifically, on perturbation direction and timing with respect to body orientation). Hence, the origin of the perturbation in relation to the walking direction and phase of gait (early, mid or late stance phase) must be considered in order to understand the coherences. In this review, we define the type of perturbation by relating the origin of the perturbation to the stance leg.

In response to **pushes** (at waist level) **in the medial direction** (i.e. the body is pushed in the medial direction with respect to the stance leg), an *outward strategy* is used by the swing leg. The foot of the contralateral (swing) leg in the subsequent step is placed further outward than the regular (unperturbed) foot placement (Hof & Duysens, 2013; Hof et al., 2010). Hof and Duysens (2013) observed changes in the EMG of the abductor muscles that are in line with the swing leg trajectory adjustments. Two responses with latencies of 100 and 170 ms and a late reaction (more than 270 ms) after the perturbation were measured in the abductor muscle of the swing leg (Hof & Duysens, 2013). This response facilitates more possibilities for foot placement (compared to normal background activation) to restore balance in response to this type of perturbation (Hof & Duysens, 2013).

In response to **pushes in the lateral direction** (i.e. the body is pushed in the lateral direction with respect to the stance leg), an inward strategy is used. The contralateral foot in the subsequent step is placed further inward than the unperturbed foot positioning of the swing leg, and increased activation of adduction muscles in the swing leg was observed (Hof & Duysens, 2013; Hof et al., 2010). Depending on the intensity and the timing of the perturbation, taking a cross-step (i.e. the swing leg trajectory crosses in front of the stance leg) might be necessary to compensate this type of perturbation (Hof & Duysens, 2013; Hof et al., 2010).

Both inward and outward strategies can be classified as stepping strategies, where the subsequent step is positioned a fixed distance away from the extrapolated COM (Hof et al., 2010). Sufficient time (at least 300 ms before touchdown) is required to apply one of these stepping strategies (Hof et al., 2010). Therefore, the ankle strategy is applied in the stance leg to initially counteract and lessen the loss of balance and provide sufficient time for adaptation of the swing leg trajectory (Hof et al., 2010).

In a similar approach, IJmker et al. (2014) investigated the influence of postural threat, such as pathways with varying width and ML pulls at waist level, during walking. Compared to unperturbed walking, step duration, step length and step width (including step width variability) were reduced in response to the highest threat condition; whereas variability of stride time and stride length increased. At the same time, EMG activity (GM, TA, BF and RF) as well as the co-contraction indices of antagonistic leg muscles were increased. In consequence, recovery to nominal gait became slower with increasing threat (IJmker et al., 2014).

Thus, with a smaller zone for foot placement, the gait pattern is characterized by shorter swing phases and single support times, which makes control of balance more challenging. With higher muscle activity, the gait is stiffer regarding the rotational leg function. This is in line with the concept of biarticular muscles being able to redirect leg forces with respect to the orientation of the leg (Sharbafi et al., 2016).

Dietz et al. (1986) observed different strategies to maintain balance in response to an **obstruction** (caused by induced external forces) **of the swing leg** that depended on the timing (i.e. phase of gait) of the perturbation. In response to perturbations at the beginning of swing, balance was mostly maintained with the support of the stance leg (Dietz et al., 1986) where an increased muscle activity (especially GM and BF) was measured. In contrast, an obstruction of the swing leg at the end of swing was compensated by an earlier touch-down of the swing leg (strong TA and RF response in the swing leg and GM and BF in the stance leg). Hence, stance leg and swing leg introduce complementary opposing rotational movements (resulting in torques acting on the trunk) that accelerate the swing leg protraction while keeping the upper body balanced. These rotational leg functions are mainly generated through biarticular muscles (GM, BF and RF) and TA (Dietz et al., 1986).

Ground level changes

When **single ground level changes** (i.e. an elevation or a drop in the ground) are introduced, the *perturbed step* is defined as the step when the touchdown is located on the altered ground level, the preceding step as the *pre-perturbed step* and the subsequent steps as *recovery steps*.

In preparation to (single) **visible drops in ground level**, the vertical GRF at take-off of the pre-perturbed step decreases with increasing drop height (Müller, Tschiesche, et al., 2014). In the stance leg, the ankle and knee are more flexed and the trunk is more erect than during unperturbed walking (Müller, Tschiesche, et al., 2014). To control the increased forward horizontal and angular momentum after landing, step length is increased (van Dieën et al., 2007). Compared to the pre-perturbed step, the perturbed step shows smaller kinematic adjustments (Müller, Tschiesche, et al., 2014). Furthermore, the touchdown behavior of the perturbed step changes from a heel-landing strategy for smaller heights to a toe-landing strategy for greater heights (van Dieën et al., 2008). It has been suggested that toe landing facilitates ankle torque control and reduces impact forces (van Dieën et al., 2008).

In response to (single) **camouflaged drops in ground level,** the magnitude of peak GRF and kinematic adjustments (e.g. reduced knee flexion) increases in the perturbed step with increasing drop height (Müller, Tschiesche, et al., 2014). Similar experiments (van Dieën et al., 2007) show that the time period between the expected and real touchdown of the foot is too short to adequately adapt leg movement and increase step length. Instead, a rapid recovery step of the trailing limb is performed to prevent falling (van Dieën et al., 2007). To date, the function of reflexes and changed muscle activation levels during the perturbed stance phase is not completely understood.

In walking over (single) **camouflaged ground level perturbations**, where touchdown occurs earlier or later than expected, van der Linden et al. (2007) identified synergies in the muscle response and assigned them to functional tasks. After delayed touchdown, ipsilateral leg muscle activation of GM and RF is enhanced, presumably to slow down forward propulsion of the body

(van der Linden et al., 2007). In response to earlier touchdown, the perturbed leg briefly stalls (larger knee flexion due to increased activity of BF and TA) to delay swing (van der Linden et al., 2007). The findings indicate adaptation of leg stiffness by changed muscle activation in the perturbed leg with greater (smaller) leg stiffness at delayed (earlier) contact. Similar adaptations of leg stiffness were found in humans running on uneven ground (Müller et al., 2010), which is in line with the concept of a generalized swing leg control in preparation for stance (Blum, Lipfert & Seyfarth, 2009).

The gait pattern (kinematics and kinetics) of **walking on stairways** (i.e. continuous change of ground level) must be reorganized from that for level walking to adjust the leg placement to the location of the stairs (Andriacchi et al., 1980; McFadyen & Winter, 1988; Nadeau et al., 2003; Protopapadaki et al., 2007). Besides step height and depth, the inclination angle also influences the gait pattern (Riener et al., 2002) as joint excursions and joint powers increase with increasing slope. Although strategies differ between ascending and descending stairways, specific mechanical patterns exist (McFadyen & Winter, 1988).

For **stair ascent**, the leg joints are more flexed at touchdown and extend more during stance than for level walking. This greater joint excursion is most prominent at the knee (Riener et al., 2002). For **stair descent**, the hip and ankle joints are extended by about 20 degrees more at touchdown and all joints flex more (by up to 70 degrees for the knee) during stance than for level walking (Riener et al., 2002).

Only the forefoot is in contact with the ground at touchdown in contrast to level walking (Riener et al., 2002). During stair ascent, forefoot contact leads to a more natural dynamic angular range of motion at the ankle, which is caused by greater knee flexion and prevents the dorsiflexor force necessary to compensate for the passive elastic plantarflexion torques (Nadeau et al., 2003; Riener et al., 2002). During stair descent, forefoot contact enables downward rotation of the foot and thus energy absorption at the ankle (Riener et al., 2002). These observations indicate that the foot function in stair walking is modified such that the ankle is able to contribute to active leg extension (increased positive power) and leg shortening (negative power). However, the ability to generate larger positive power during stair ascent is limited (Riener et al., 2002). Surprisingly, maximum ankle torques are clearly lower for stair walking than for level walking (Riener et al., 2002) suggesting power-amplifying foot mechanisms in human walking (Lipfert, Günther, Renjewski & Seyfarth, 2014).

The knee most significantly contributes to leg shortening (descent) and leg extension (ascent) during stance with large positive and negative joint power, respectively (Riener et al., 2002). The knee largely accounts for the change in potential energy, which is in line with other findings (Andriacchi et al., 1980; McFadyen & Winter, 1988; Nadeau et al., 2003; Riener et al., 2002). Thus, the knee overcomes the changes in step height on stairs by adjusting the system energy. While the contribution of the hip is smaller (reduced extension moments) during stair ascent than during level walking, only hip flexion moments occur during stair descent. Neither the positive nor the negative hip power (and the resulting energy contributions) in stair walking exceeds the hip power in level walking. Thus, the hip does not play a major role in compensating for the altered energy requirements of stair walking. In addition, negative work and negative power actually decrease with the increasing slope of stair descent (Riener et al., 2002)

indicating the possibility that adjustments at the hip during stair walking are required for other tasks such as postural balance or swing leg placement.

In both the hip and ankle, joint torques are smaller for stair walking than for level walking. This might be due to the shorter step length during stair walking which requires less leg rotation (swing leg protraction and leg retraction). Moreover, although the positive joint power at the hip and ankle is smaller during stair walking, the ankle exhibits larger negative joint power than during level walking.

In summary, all three leg joints contribute quite differently to stair walking. Energetically, the knee largely supports stair ascent and descent, the ankle mainly supports stair descent, and the hip does not show any greater joint torque or joint power than for level walking.

Compared to unperturbed walking, stable locomotion is realized during **walking on uneven terrain** (i.e. continuously changing ground level heights) by adaptations in stepping strategy, increased muscle activity and increased hip work (Voloshina et al., 2013). This includes shorter step length and greater joint work (e.g. knee and hip) and metabolic energy expenditure. In a simulation study based on the spring-loaded inverted pendulum (SLIP) model, Rummel et al. (2010) suggested there is lower leg stiffness and flatter angles of attack when walking on uneven terrain to achieve greater system robustness. In this context, the more crouched leg posture observed in walking on uneven ground (Voloshina et al., 2013) might increase leg compliance and provide a smoother gait, although at higher energetic costs. This was represented in an extended model with segmented legs where leg stiffness largely depends on the amount of leg flexion (Rummel & Seyfarth, 2008).

Slopes

Adaptations of gait patterns and leg parameters are necessary for stable and safe locomotion when walking on positive and negative slopes.

In comparison to level walking, the gait pattern during **walking on inclined ground** shows slightly reduced cadence (McIntosh et al., 2006; Sun et al., 1996). With respect to adaptations in walking speed and step length, contrasting results (i.e. either an increase or decrease) have been obtained (Leroux et al., 2002; McIntosh et al., 2006; Redfern & DiPasquale, 1997; Sun et al., 1996). This discrepancy may be due to differences in the experimental designs and the normalization methods.

The gait pattern reveals that – compared to level walking – the ankle joint is more dorsiflexed during stance (Lay et al., 2006; Leroux et al., 1999; McIntosh et al., 2006). Also the roll-over mechanism (of the knee-ankle-foot system) changes to a more dorsiflexed ankle-foot configuration in relation to the inclination level and hence contributes to sustaining a balanced vertical orientation in space (Hansen et al., 2004). In addition, peak knee extensor moments (at early mid stance) and peak hip extensor moments and their duration (until late stance) are higher than for level walking (Lay et al., 2006).

During the **transition from level to incline walking**, swing limb kinematics show two adaptations: an initial response to ensure toe clearance by increased hip flexor activity (Lay et al., 2006; Prentice et al., 2004), and later changes ensuring an elevated foot contact. This is supported by energy absorption (Prentice et al., 2004) and larger joint flexion at the hip (Leroux

et al., 1999; McIntosh et al., 2006; Prentice et al., 2004) and knee (Lay et al., 2006; Leroux et al., 1999; McIntosh et al., 2006) during late swing.

During **walking on negative slopes**, changes in gait pattern, leg parameters and joint powers and moments are similar but inverted compared to the corresponding changes when walking on positive slopes. Inconsistent results for spatiotemporal parameters of the gait pattern have been reported: McIntosh et al. (2006) observed longer stride lengths for downhill walking barefoot, whereas Leroux et al. (2002) observed shorter stride lengths for downhill treadmill walking than for level walking. Other studies (Kawamura et al., 1991; Redfern & DiPasquale, 1997; Sun et al., 1996) reported shorter step lengths and step periods for walking on negative slopes. These discrepancies may originate from different surface friction conditions (Sun et al., 1996) or some other reasons.

Compared to level walking, ankle plantar-flexion (Kuster et al., 1995) and knee flexion (Hansen et al., 2004; Kuster et al., 1995; Lay et al., 2006) in the support limb were greater for downhill walking. Moreover, lower hip flexion angles were measured in early stance and late swing (Kuster et al., 1995; Lay et al., 2006; McIntosh et al., 2006) but slightly larger hip flexion angles were found during the mid-stance phase (Kuster et al., 1995; Lay et al., 2006).

Kinematic changes indicate compensation of the slope by greater knee flexion from early stance to early swing and more extended hip from early swing to early stance (Kuster et al., 1995). This result is supported by data on changes of the roll-over configuration in relation to the negative slope (Hansen et al., 2004). The authors (Hansen et al., 2004) also describe a more plantar-flexed orientation of the knee-ankle-foot roll-over configuration provided by changes (greater flexion) in knee function. Moreover, knee power and torque curves in the stance limb are significantly higher indicating primarily eccentric (power absorption) muscle work (Kuster et al., 1995; Lay et al., 2006). To date, the effect on leg stiffness and joint stiffness behavior of walking on slopes has not been investigated.

Compared to level walking, the gait pattern on slopes (uphill and downhill) is adapted by postural adjustments (e.g. extended ankle for downhill slopes and trunk flexion for uphill slopes), and energy supply and absorption (mainly at the knee) by pronounced knee extension and flexion in uphill and downhill slopes (Hansen et al., 2004; Kuster et al., 1995; Lay et al., 2006; Redfern & DiPasquale, 1997).

Moving ground

Perturbations of walking due to moving ground can occur in the three anatomical directions, i.e. AP, ML and distal-proximal. In this section, we first present results on perturbations in the AP direction and then in the ML direction (see Table 2.3).

Backward translations of the ground during walking cause displacements of the ankle angle (greater dorsiflexion) and more forward body orientation from the ankle to the COM (Nashner, 1980). The response to this perturbation consists of changes in ankle extension moments that coincide with large increases in GM muscle activity (Nashner, 1980) resulting in normal joint configuration at the end of the step cycle.

Forward translations of the ground during walking cause displacements of the ankle angle (lower dorsiflexion) in the leading stance leg and more backward body orientation from the

ankle to the COM (Nashner, 1980). These perturbations are compensated by joint flexion moments (Ferber et al., 2002; Nashner, 1980) and higher EMG activity in the TA and almost no EMG activity in the GM (Nashner, 1980). Complementary results were found by Yang and Pai (2010), who observed greater hip extension and knee flexion torques and lower ankle plantar flexion in the stance limb during slipping (i.e. a sudden forward displacement of the foot).

Subjects respond to sudden ground movements in the AP direction with changes in ankle torques (relative to the perturbation) to prevent further displacement of the foot (relative to the COM) and increases in hip and knee torques to realign the body posture in order to maintain balance and locomotion. Tang et al. (1998) emphasized the importance of inter-limb coordination to cope with sudden ground changes and suggest that postural activity from distal leg muscles and additional coordination between the two lower limbs may be the key to reactive balance control in forward slips. In the unperturbed condition, the leg axis is defined by the foot landing position and the movement of the COM. This results in a rotation of the leg axis (leg retraction) that needs to be restored in the perturbed case. The biarticular thigh muscles (RF and BF) and the ankle dorsiflexor (TA) are able to actively adjust the orientation of the leg axis on moving ground (Tang et al., 1998). This supports a return to leg retraction (and hip extension) after the initial perturbation phase (with interrupted hip extension during the first 250 ms after perturbation) (Tang et al., 1998).

While **continuous ground translations** (in ML direction) where introduced, two different coping strategies were observed during treadmill walking: fixing the body in space and fixing the body to the base (Brady et al., 2009). To fix the body in space (FIS), subjects let the treadmill move beneath them with less effect on their trunk position but more on their step width. Left foot steps were wider when the base moved to the right and narrower when moved to the left. To fix the body to the base (FTB), the subjects' entire body moved with the base either not affecting their step width significantly (Brady et al., 2009). In similar studies, ML perturbations were compensated by greater step width (Hak et al., 2013; Sari & Griffin, 2014) and step frequency (Sari & Griffin, 2014), concomitant with shorter step length and slower walking speed (Hak et al., 2013).

When **single ground perturbations** (in ML direction) were applied to the right leg during stance, three different strategies were observed for adjusting swing leg positioning of the subsequent step: 1) inward foot placement, 2) outward foot placement, and 3) early touchdown (Oddsson et al., 2004). In response to backward-left ground translations, balance was maintained by a more pronounced inward foot placement (strategy 1). To cope with forward-right translations either the step width was increased (strategy 2) or step length was decreased (strategy 3). All three strategies are intended to modulate moment arms to maintain the COM within the BOS hence realigning posture and normal gait was achieved after three consecutive steps (Oddsson et al., 2004).

Obstacles

During everyday activities, humans may stumble or trip due to swing leg blockade caused by obstacles that are within the swing leg trajectory (or others). In this scenario, humans apply two different coping strategies: raising or lowering the swing limb (Cordero et al., 2003; Eng et al., 1994; Schillings et al., 2000).

Perturbations in early swing and mid-swing are mostly compensated using the elevating strategy (Cordero et al., 2003; Eng et al., 1994; Schillings et al., 2000). Here, the leg is quickly lifted after swing leg perturbation in order to overcome the obstacle and the swing phase is continued. Step length (foot relative to COM) is increased to ensure sufficient time to recover during the next double stance (Cordero et al., 2003, 2004; de Boer et al., 2010; Eng et al., 1994; Grabiner et al., 1993; Schillings et al., 1996, 2000). The lowering strategy is used to compensate for perturbations during mid-swing and late swing (Cordero et al., 2003; Eng et al., 1994; Schillings et al., 2000). This strategy is characterized by a smaller, quicker step (shorter step length and swing) most commonly followed by a few consecutive recovery steps (Cordero et al., 2003, 2004; de Boer et al., 2010; Eng et al., 1994; Schillings et al., 2000).

In both responses (elevating and lowering strategy), the stance leg contributes to the recovery with fast increases in joint torques (mainly ankle strategy), which reduces the forward angular momentum of the body (Pijnappels et al., 2005). This leads to ankle plantar flexion and knee and hip extension (Pijnappels et al., 2005) raising the COM and providing sufficient time for swing leg adjustments. A model focusing on minimization of costs based on the required torque, impulse, power, and torque/time showed similar (humanlike) strategy preferences to those described above (de Boer et al., 2010).

2.3.4. Response to perturbations while running

Running is one of the fastest human gaits, and humans can keep up running speed despite sudden or unforeseen environmental influences. In this section, we review responses to external perturbations by *ground level changes* and *changing ground properties*.

Ground level changes

Similar to the section on Walking, when (single) **ground level changes** (i.e. elevation or drop in the ground) are introduced during running, the *perturbed step* is defined as the step with touchdown on the altered ground level, the preceding step is defined as the *pre-perturbed step* and the subsequent steps as *recovery steps*.

While adaptations of gait and leg parameters already take place in the pre-perturbed step (similar to the findings in perturbed walking trials – see section on Walking) for expected perturbations, no adaptations in the pre-perturbed step were observed for unexpected perturbations (Ernst et al., 2014; Grimmer et al., 2008; Müller et al., 2012).

For expected ground level changes, adaptations in the pre-perturbed step are in relation to the perturbation direction, i.e. taking a step up or down. Compared to level running, increases in leg stiffness and vertical COM velocity were measured in preparation for upward steps (Ernst et al., 2014; Grimmer et al., 2008). In preparation for downward steps, leg stiffness is lower than during level running, which results in less COM oscillation (Ernst et al., 2014; Müller et al., 2012).

Adjustments of leg parameters (leg length, leg stiffness and angle of attack) as well as GRF in the perturbed step are in relation to the direction and length of the perturbation such as ground level elevations and drops (Müller & Blickhan, 2010). Leg stiffness, angle of attack, and GRF

decrease with increasing elevation height (Grimmer et al., 2008; Müller & Blickhan, 2010; Müller et al., 2010), whereas they increase with increasing drop height (Müller & Blickhan, 2010; Müller et al., 2012). Similarly to leg stiffness, ankle stiffness is adjusted to perturbation height (Müller et al., 2010). Furthermore, while leg length is reduced when stepping up, leg length is not increased when stepping down (Müller & Blickhan, 2010). The lack of leg lengthening in response to ground level drops may be explained by the characteristics of a running gait including a forefoot strike pattern. Supplementary findings from simulations predict similar leg behavior to that described above (i.e. the change in leg parameters with drop height) to keep running speed constant (Ernst et al., 2009).

The magnitude of leg parameter adjustments also depends on the perturbation magnitude and direction. The described adjustments in leg stiffness for the (pre-)perturbed steps are in accordance with simple SLIP-model simulations (Grimmer et al., 2008). Moreover, increases in angle of attack, leg length and resulting swing leg retraction describe a strategy for running across uneven ground (Müller et al., 2012). The described adaptations enhance the stability of a running spring mass system and improve its capability to compensate for differences in apex height between steps (Seyfarth et al., 2003). In this context, Müller et al. (2010) assumed that while pre-activation control plays a major role in preparing for the compensation of altered ground properties, muscle activation control is less important in stance because geometry and initial condition ensure adequate adjustment of joint and leg stiffness (Müller et al., 2010).

Adjustments of the recovery step depend on the subsequent environmental conditions: either further changes in ground level (which might be seen as ongoing or additional perturbation) or no further ground level changes (i.e. unperturbed running on the new level). Among others, the first condition is discussed in the section on ground level changes introduced in the perturbed step. With respect to the latter condition, adjustments of the COM are mostly completed after one step on the new level (Ernst et al., 2014). Necessary adaptations already take place while the foot returns to the ground for single ground level perturbations (up or down) (Ernst et al., 2014). It is suggested that adaptation of leg parameters to control the COM oscillation might be a general control principle in running (Ernst et al., 2014).

In a study by Voloshina & Ferris (2015) comparing subjects running over **even and uneven terrain**, no significant changes in running kinematics were observed, but significant increases in step parameter variability were found. Their results showed hardly any variation in mechanical work at the knee and the hip, but reduced mechanical work on the limb and reduced joint torque at the ankle.

In both walking and running, almost half of the energy increase is related to additional positive and negative mechanical work for steps varying in height by up to 3.8 cm (Voloshina & Ferris, 2015). However, while the remaining additional work was attributed to a less efficient muscle function due to uneven ground, this assumption has yet to be proven.

In this section, review of studies on ground level perturbations showed that the mechanical responses differ for single and continuous perturbations (e.g. uneven ground). At smaller ground level height differences (2.5 to 3.8 cm on uneven ground), the kinematics and kinetics remain largely invariant compared to even ground conditions. These observations are in line with results of biomechanical running models (Rummel & Seyfarth, 2008) indicating that smaller ground level differences can be tolerated without the need to adapt leg parameters.

Changed ground properties

Running over ground with varying properties (e.g. elastic or damped surfaces) requires adjustments in leg parameters for stable locomotion. Decreases in ground stiffness (softer surfaces) result in greater leg stiffness (Ferris et al., 1998; Kerdok et al., 2002) and may decrease the runners' metabolic rate (Kerdok et al., 2002) compared to solid ground. Correspondingly, running on harder surfaces results in lower leg stiffness (Ferris et al., 1999, 1998). Larger peak angular velocities in the hip, knee and ankle were observed for running on stiffer surfaces (Hardin et al., 2004). In addition, the leg configuration is more extended (less hip and knee flexion) at initial contact (Hardin et al., 2004).

Ferris et al. (1998) argued that runners adapt their effective vertical stiffness (sum of leg stiffness and surface stiffness) during running on surfaces with different properties to maintain similar running mechanics. This adjustment in leg stiffness enables smooth transitions between different properties and ensures that the COM excursions during locomotion remain similar (Ferris et al., 1999). In a simulation study, Hurst et al. (2007) introduced sudden changes in surface stiffness to a segmented leg model with a compliant knee. Similar to experimental findings (Ferris et al., 1999, 1998; Kerdok et al., 2002), a greater ground compliance causes an increase in the predicted leg stiffness of the model indicating a potential contribution of leg segmentation to stiffness adaptation without the need for sensory feedback and advanced control approaches. A similar observation was found in a muscle-skeletal simulation study concerning hopping on compliant ground (van der Krogt et al., 2009, see section on Hopping) where greater leg stiffness was predicted for hopping on softer ground.

Running on sand (a damping substrate) requires 15 % more mechanical work and 1.6 times more energy expenditure than running on solid ground (Lejeune et al., 1998). Comparing running on sand with firm surfaces, other studies (Alcaraz et al., 2011; Pinnington et al., 2005) observed shorter stride length, longer stance time, and a phase shift (~5 % of stride duration) of joint kinematics during the gait cycle. Furthermore, the knee and hip are more flexed at initial foot contact, mid-stance, and take-off (Alcaraz et al., 2011; Pinnington et al., 2005) resulting in a lower COM position and a greater forward trunk lean than during running on a firm surface (Alcaraz et al., 2011).

Furthermore, Pinnington et al. (2005) found higher energy costs while running on sand and attributed this to greater muscle activity controlling the knee and hip during stance and swing. While vastus (lateralis and medialis), rectus femoris and tensor fascia latae muscles were more active in stance, the hamstring muscles were more active during both stance and late swing (Pinnington et al., 2005), which is similar to the change in muscle activity when running on uneven ground (Voloshina & Ferris, 2015).

2.3.5. Response to perturbations while hopping

In this section, we review hopping (i.e. hopping on the spot) regarding elastic or damped ground properties (see Table 2.4).

Moritz and Farley (2003) showed that humans mimic spring-like leg behavior in the leg-surface relationship to maintain relatively constant COM motion while hopping on damping ground. Thus, non-spring-like surface properties are compensated by non-spring-like leg behavior. The authors (Moritz & Farley, 2003) measured greater positive leg work (65 % more extended leg during take-off than leg compression during landing) and 24-fold higher net work compared to an elastic surface.

For continuous hopping on soft (but still elastic) surfaces, the leg stiffens (Farley et al., 1998; Ferris & Farley, 1997), and ankle torques and knee extension increase (Farley et al., 1998). In contrast, during hopping on hard (but still elastic) surfaces, the leg softens and ankle and knee flexion increases (Moritz & Farley, 2004). While hopping on stiffer surfaces, hoppers extend their legs in early stance and compress their legs in late stance leading to normal COM dynamics but higher muscle activation levels (Moritz & Farley, 2005).

When the surface property expectedly switches from soft to hard, hoppers pre-flexed their knee and pre-activated muscles to be prepared for the change in surface stiffness (Moritz & Farley, 2004). Similar observations were made in simulations of sudden changes in surface stiffness (van der Krogt et al., 2009): a change from hard to soft ground requires softening of the leg, and a change from soft to hard ground requires stiffening of the leg to maintain steady-state hopping.

These adaptations in leg stiffness and mechanics to different surface stiffness and damping properties are similar to adaptations observed for running (see section on Running).

2.4. Conclusion

Irrespective of the motion task, controlling the forward momentum of the trunk is fundamental for maintaining balance control, recovering balance, and hence preventing falling (Cordero et al., 2004; Grabiner et al., 1993; Henry et al., 1998a; Yang et al., 1990). Observing responses to perturbations provides insights into counteractive body movements and can be used to identify postural control strategies (Runge et al., 1999).

The results of this review clearly show that humans respond to sudden perturbations deflecting the COM by the sequential generation of ankle, knee and hip torques (joint strategy) contributing to trunk control. When the joint strategy (change in joint torques) is insufficient, the leg position must be re-adjusted relative to the COM to realize an efficient response to the perturbation. These strategies are termed foot placement strategies (FPS). Oddsson et al. (2004) stated that FPS are intended to modulate moment arms to maintain the COM within the BOS thereby realigning posture. However, in FPS biarticular muscles seem to play an important role (Dietz et al., 1986; IJmker et al., 2014; Tang et al., 1998). In this context, ankle strategy in the support limb is not only used as a quick response to maintain (or achieve) balance but also to provide sufficient time for modified foot positioning and adjustment of the swing leg trajectory. Thus, muscle weakness in the lower extremities (Daubney & Culham, 1999) or larger leg muscle asymmetries regarding strength and power (Skelton, Kennedy & Rutherford, 2002) are potential indicators of an increased risk of falling.

This review presented motor control strategies for coping with external perturbations. Similar adjustment patterns were found for coping with similar perturbations during different motion tasks:

- For walking on (single or multiple) steps or slopes, the control of the COM height (lifting or lowering to a new level) plays a major role, and changes at the ankle and knee are critical.
- For standing and walking, a distal-to-proximal cascade of kinematics and EMG activation patterns was found in response to ground perturbations (e.g. surface translations in the transversal plane).
- For locomotion on changing ground properties including elasticity and damping, humans adapt leg stiffness in relation to surface stiffness for both running and hopping. However, only a few studies (Lejeune et al., 1998; Marigold & Patla, 2005) are available concerning walking on ground with changing properties.
- For walking, biarticular leg muscles (such as BF, RF, and GM) play a major role in posture control (e.g. regulate body sway or compensate horizontal perturbations) and quick adaptations of FPS.

Relevance to daily activities

The literature review outlined balancing and coping mechanisms and strategies employed by healthy persons in responding to selected mechanical perturbations to prevent imbalance and falling. In some cases, the specific responses to perturbations summarized in this review may be relevant for daily activities because some of the described perturbations are similar to reported causes of fall-related injuries (see Figure 2.1, B and Table 2.5, filled circles).

Unfortunately, not all relations between perturbations and reasons for falling could be considered in this review (Table 2.5, half-filled circles). Several critical conditions have not yet been studied (e.g. response to perturbations when walking on icy stairs or slopes) indicated by open circles in Table 2.5.

In the following, as examples we will identify some relations between external perturbations and causes of fall-related injuries. For instance, there are relevant relations for the perturbation ground level changes and the daily activities of walking on stairs and walking on other surfaces. Two studies of men (mean age, 57 years) and women (mean age, 43 years) showed that on average between 47 to 66 steps are taken on stairs every day (Lee & Paffenbarger, 2000; Purath, Michaels Miller, McCabe & Wilbur, 2004). Although this is a small number compared to 6500 walking steps per day (Tudor-Locke & Bassett, 2012), 12 % of fall-related injuries happen during stair walking (Do et al., 2015).

Moreover, the ground changes on slopes is related to the context of other surfaces. Depending on the inclination angle, slopes increase the cost of transport in walking (Minetti, Moia, Roi, Susta & Ferretti, 2002). However, the elderly (55 to 75 years) reduce their walking speed to a greater extent than younger persons (10 to 55 years) with increasing inclination (Sun et al., 1996). The reduction of walking speed may not only be due to the lower physical capacity but also to a compensating strategy for avoiding a higher risk of falling. In addition, amputees struggle to walk on slopes because of a limited range of motion and power generation restricting their compensation potential (Vickers, Palk, McIntosh & Beatty, 2008).

Table 2.5: *Relation between reviewed research fields according to the PMA (perturbation matrix) and causes of falls during daily activities. Circles (half-filled or fully filled) indicate that external perturbations are similar to causes of falls, whereas open circles indicate perturbation conditions which have not yet been studied. AP: anterior-posterior direction, ML: medio-lateral direction, V – vertical direction.*

Perturbations		Falling context during daily activities			
Type	Feature	Walking on stairs	Walking on snow & ice	Walking on other surfaces	Other contexts
Ext. Forces	Location *(joint, region…)*	○	○	○	◐
Ground Changes	Ground level (up/down)	●	◐	●	◐
	Slopes *(up/down, ML)*	○	◐	●	○
	Deformation (elastic/damped)	○	◐	●	◐
	Structure *(friction)*	○	●	◐	○
	Moving *(AP, ML, V)*	○	○	●	○
	Obstacles	●	◐	◐	●

Outlook and limitations

In accordance with the intended goals of this review, we highlighted several areas of research (see Table 2.3 and Table 2.4) and outlined common observations. Comparing relevant studies was challenging because the reviewed studies show selected data (kinematics, kinetics, and/or EMG) and relevant results regarding specific research questions. Therefore, we occasionally had to compare and combine findings from different literature articles to obtain sufficient evidence to extract plausible conclusions.

In the future, the PMA could be modified by removing selected exclusion criteria (e.g. considering clinical studies and investigations on responses of the central nervous system), by gait), and extending and varying (voluntary) perturbations (e.g. turns and spins as well as locomotion speed and gait initiation). Furthermore, the response to changes of locomotion speed may be an important parameter with a direct relation to daily activities. For instance, the elderly (61 years) had wider step widths than younger subjects (25 years) when walking at the same speed (Hurt, Rosenblatt, Crenshaw & Grabiner, 2010). However, at preferred (self-selected) walking speed, no difference in step width from younger adults was found (Elble, Thomas, Higgins & Colliver, 1991) indicating that the definition of locomotion speed can clearly change the gait characteristics when compared to self-selected speeds.

In our review, we considered studies on human locomotion under challenging conditions, specifically with external mechanical perturbations. The PMA reflects publications fulfilling the predefined inclusion and exclusion criteria (see Table 2.2) for standing and walking (see Table 2.3) as well as running and hopping (see Table 2.4). The PMA clearly shows the need for future research directions in areas that have not been (sufficiently) considered. Furthermore, the PMA may be extended by including additional motion tasks and perturbations.

The second goal of this review was to identify balance mechanisms and strategies that are applied to prevent imbalance and falls. The results described in this review may be relevant for:

- developing humanlike coping mechanisms for applications in assistive devices or robots;
- implementing coping strategies for behavior control of assistive devices to predict mechanical responses;
- transferring indications and major insights to preventive training to reduce the risk of falling; and
- developing rehabilitation strategies for clinical interventions on balance impairments (e.g. after stroke).

Considering the comparison of well-covered fields in the PMA and fall-related injuries during daily activities, we observe that not all of our detected connections are covered in this review. Nonetheless, we believe that this review helps to improve the understanding of human balance strategies, underlying balance mechanisms and motor control to cope with unexpected perturbations. Insights from this review may be applied as a basis for modifying assistive devices such as exoskeletons that are used for rehabilitation and contribute to improving the quality of life in the elderly and impaired.

3. Importance of biarticular leg muscles for maintaining balance during perturbed upright human standing

3.1. Introduction

Human bipedalism is characterized by an upright trunk posture and straight knee configuration during stance phases. The trunk must be balanced during movements such as walking and running. This is an ongoing task also during standing as the body sways and has to be balanced. This postural behavior pursues two main goals: postural orientation and postural equilibrium (Horak, 2006b). Postural orientation requires active alignment of the trunk and head in relation to gravity, support surfaces, as well as visual and internal references. Postural equilibrium requires movement strategies (such as ankle or hip strategy) to be coordinated for center of mass (COM) stabilization during self-initiated or externally triggered disturbances of stability (Horak, 2006b). Typically, humans control ankle and hip (joint strategies) to achieve and maintain a stable upright posture (Loram, Maganaris & Lakie, 2004; Runge et al., 1999; Winter, Patla, Prince, Ishac & Gielo-Perczak, 1998; Winter, Patla, Rietdyk & Ishac, 2001). Alternatively, they can also use a stepping strategy, which involves taking a step to relocate the center of pressure (COP) (Mille et al., 2003).

Studies (Doorenbosch, Harlaar & van Ingen Schenau, 1995; Doorenbosch & van Ingen Schenau, 1995; Hof, 2001; Jacobs & van Ingen Schenau, 1992) show that during upright stance the modes of action of monoarticular leg muscles are directed along the leg axis in the vertical direction, whereas the modes of action of biarticular leg muscles are mostly directed transversely to the leg axis in the horizontal direction. In this way, biarticular muscles control the distribution of net moments and therefore the direction of the external GRF whereas monoarticular muscles mainly generate positive work (Jacobs, Bobbert & van Ingen Schenau, 1993; Jacobs & van Ingen Schenau, 1992; van Ingen Schenau, Boots, de Groot, Snackers & van Woensel, 1992). This means that GRF can be redirected to maintain an upright posture (according to the virtual pendulum concept (Maus et al., 2010)), retain balance, and avoid falling in response to external perturbations such as horizontal pushes and pulls. In this context, Günther, Grimmer, Siebert and Blickhan (2009) evaluated the contribution of leg joints to an upright posture in quiet stance. They found that biarticular leg muscles may function effectively to stabilize quiet stance and counteract fluctuations around static equilibrium.

Recent research (Rode & Seyfarth, 2013) demonstrates that a model with appropriate segment length (1:1 thigh to shank length ratio, see Figure 3.1, A) and moment arm ratios of two-joint muscles (2:1 for hip vs. knee, and for ankle vs. knee) may uncouple postural control (via biarticular muscles) from axial leg force production (via monoarticular muscles). Moreover, experimental results (Tokur, Rode, Hoitz & Seyfarth, 2015) suggest that this uncoupling is also valid in perturbed upright human standing. This conceptual design has already been applied and successfully tested (Sharbafi et al., 2016), showing that posture control via biarticular leg muscles can simplify control and reduce energy consumption.

Through the activation of biarticular leg muscles humans may be able to manipulate leg forces perpendicular to the leg axis, which requires appropriate leg segment lengths and muscle

moment arms, similarly found in humans (Rode & Seyfarth, 2013). To further investigate the role of biarticular muscles, the goal of this work is to experimentally assess the relevance of this concept for humans by following the conceptual work of Rode and Seyfarth (2013). Changes of leg muscle activation in response to horizontal and vertical perturbations (constant external forces) while standing upright are investigated. In this way, the understanding of the contribution of mono- and biarticular leg muscles to maintaining postural balance can be improved. It is hypothesized that quasi-linear relationships exist between (i) introduced perturbation forces, (ii) initial leg configuration (knee angle), (iii) combined effect of perturbation force and leg configuration, and corresponding changes in electromyography (EMG) activation of selected muscles. These should be in line with predictions provided by the conceptual model (Rode & Seyfarth, 2013).

3.2. Method

Twelve subjects (6 male, 6 female) participated in an experimental study on perturbed upright human stance. Subjects were asked to maintain their posture in the face of external horizontal forces. Subjects were instructed to use leg muscles to counteract the resulting torques (from the perturbations) without active trunk extension or flexion or compensatory arm movements.

Average subject characteristics are shown in Table 3.1. The study was approved by the Ethics Committee of Technische Universität Darmstadt (in accordance with the Declaration of Helsinki) and written informed consent was provided by all subjects prior to the experiment. None of the participants reported any current case of locomotor deficit. Subjects were barefoot and sample perturbations were conducted to familiarize them with the different types of perturbation.

Table 3.1: *Characteristics of each subject (#) and the grand mean (∅) including standard deviation (± SD).*

#	age *[yrs]*	height *[m]*	mass *[kg]*	sex
1	*21*	*1.78*	*74.43*	M
2	*23*	*1.83*	*91.24*	M
3	*25*	*1.85*	*82.71*	M
4	*25*	*1.67*	*62.15*	F
5	*22*	*1.65*	*60.50*	F
6	*25*	*1.79*	*69.81*	F
7	*21*	*1.65*	*62.33*	F
8	*24*	*1.84*	*94.80*	M
9	*24*	*1.80*	*81.71*	M
10	*23*	*1.72*	*67.42*	F
11	*24*	*1.78*	*71.48*	M
12	*20*	*1.72*	*67.35*	F
∅	**23.08** *(± 1.42)*	**1.76** *(± 0.06)*	**73.83** *(± 9.29)*	

3.2.1. Experimental design

Subjects were asked to stand in an upright and stable posture defined as the *initial position* with their trunk between two bars (one in front and one behind) to visually and physically limit their space for trunk flexion and extension. The bars were adjusted to the individual posture. The initial position served as an *extended* knee configuration characterized by an inner knee angle of about 180°. Two more knee configurations were defined: *intermediate* (~155°) and *bent* (~140°). This results in different leg configurations consisting of stance leg (single- or two-legged) and knee angle (extended, intermediate or bent). Perturbations were introduced at the shoulder/neck region and right ankle (Figure 3.1, red arrows in B and C). When perturbations were introduced at the right ankle, subjects stood only on the left leg so that the right leg was free to swing and introduce perturbations. During ankle perturbations, subjects were asked to not only maintain an upright posture, but also to fix their right ankle position parallel to the left ankle (sagittal plane).

To ensure that the leg configuration was maintained during the measurements, a laser pointer was fixed to the left thigh. The laser beam was projected onto the wall in front of the subjects by a mirror on the floor. The projection of the laser beam was marked for each leg configuration (stance leg and knee angle) and served as a visual control during the measurements.

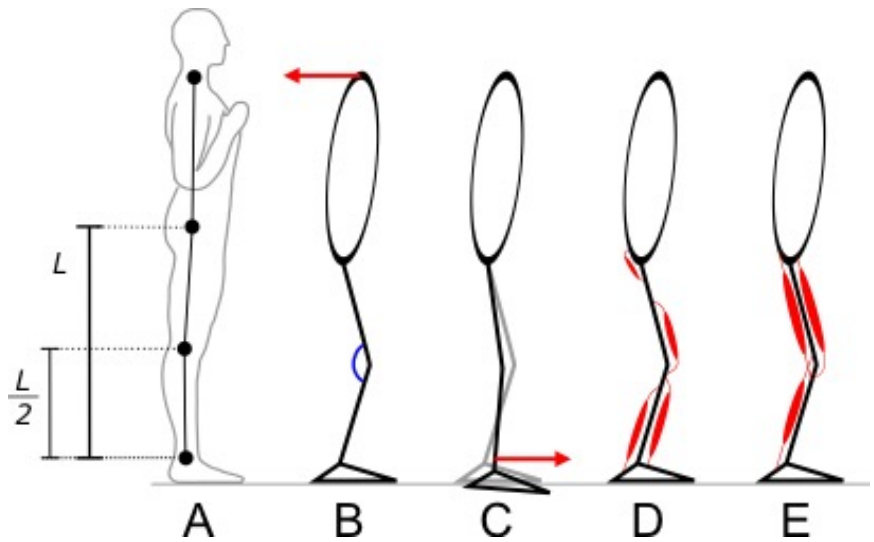


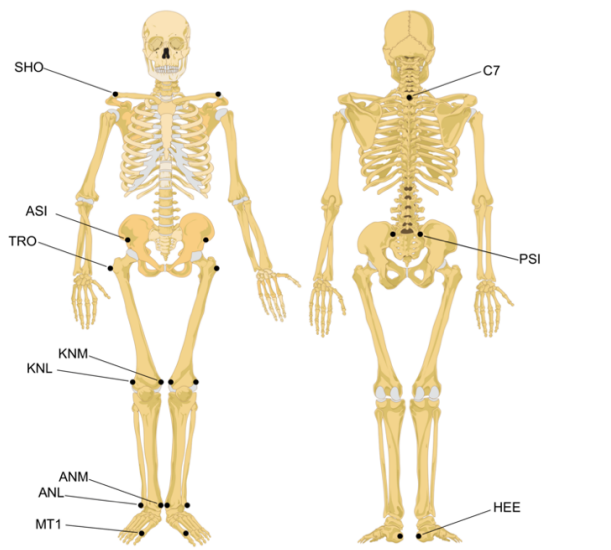
Figure 3.1: *Three-segment model and experimental design. A: Human body with indicated segments and leg length (L) and thigh to shank ratio. B: Upright posture and knee angle under consideration (inner angle between thigh and shank, blue line) with perturbations at the neck (red arrows). C: Upright posture with perturbations at the ankle (red arrows at free, swinging black limb). D+E: positions of selected mono- (D) and biarticular (E) muscle groups, details are given in Section 3.2.2.*

Perturbations were applied manually by constantly pulling (horizontally in the sagittal plane) a rope attached to the subject's body. To achieve a quasi-static perturbation, the pulling force was permanently visualized and controlled by an attached mechanical force gauge. Furthermore, a mechanism to suddenly release the perturbation was attached to the rope. Each measurement lasted 15 s and consisted of three parts: initial phase (IP) – no perturbation (1 – 5 s); perturbation phase (PP) – introduction of quasi-static perturbations (5 – 10 s); and recovery phase (RP), i.e. release of the perturbation and recovery of the initial posture (10 – 15 s).

With respect to the different perturbation locations (shoulder/neck region and ankle) and different perturbation directions (anterior and posterior), there were four different experimental conditions: ankle-anterior (AA), ankle-posterior (AP), shoulder-anterior (SA) and shoulder-posterior (SP). Perturbations consisted of different pulling forces (10 N, 20 N, 30 N) in different directions (anterior and posterior direction). Additionally, trials with perturbations in the vertical direction (VD) were conducted resulting in a fifth experimental condition. For the VD condition, the measurement protocol was the same as the other conditions, except for the perturbations. Instead, bags (simulating external downward pulling forces of 30 N, 60 N, 90 N) of appropriate weight on either side were handed to the subjects during the measurement. The two bags had to be held during the PP and then released by the subject. Both experimental conditions and perturbation intensities (i.e. amount of N) were randomized.

3.2.2. Data acquisition

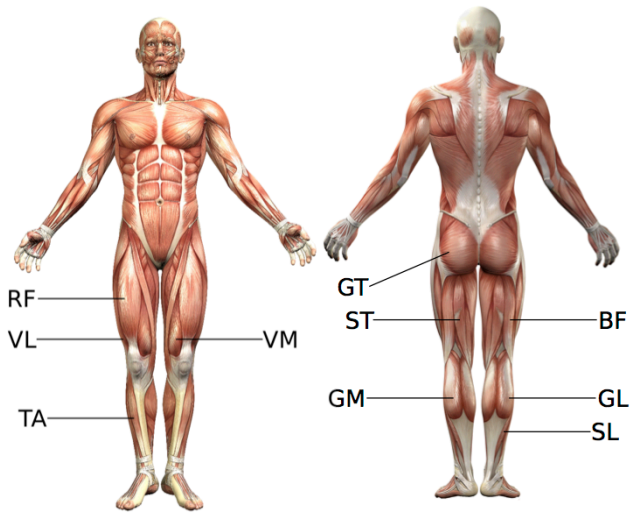
Three-dimensional (3D) whole-body kinematics and kinetics were collected in this experiment. Ground reaction force (GRF) data were collected using a force plate (type 9260AA6, Kistler, Winterthur, Switzerland) with 1000 Hz sampling frequency. Kinematic data were collected via 10 high-speed infrared cameras (Oqus 300 and 350+, Qualisys, Gothenburg, Sweden) with a sampling frequency of 250 Hz and were upsampled to 1000 Hz for later analyses. The cameras recorded 3D positions of 21 reflective markers placed over anatomical landmarks on the whole body (see Figure 3.2). Markers were stuck to the skin using double-sided tape and were additionally secured with adhesive tape to assure good fixation regardless of sweat or impact vibrations. Additionally, an HD webcam (Microsoft LifeCam Cinema, 720 p, 30 Hz) was synchronized to the motion tracking system.



Marker	Anatomical landmark
	Trunk
C7	7th cervical vertebra
SHO	Acromion
ASI	Anterior superior iliac spine
PSI	Posterior superior iliac spine
	Legs
TRO	Greater trochanter
KNL	Lateral epicondyle
KNM	Medial epicondyle
ANL	Lateral malleolus
ANM	Medial malleolus
	Feet
HEE	Calcaneus
MT1	1st metatarsal head

Figure 3.2: *Anatomical landmarks for marker placement. Markers are indicated by black dots on the human skeletons on the left (adapted from Clker-Free-Vector-Images (2017a, 2017b)). Indices and marker locations are specified on the right.*

Surface EMG data of 16 selected mono- and biarticular muscles of the lower limbs (see Figure 3.1, D + E and Figure 3.3) were measured with an EMG system (DELSYS, Bagnoli 16000) and corresponding software using parallel-bar EMG sensors[3]. The EMG of lower leg muscles were only measured in the left leg. Sensors were applied to each muscle according to SENIAM (Surface ElectroMyoGraphy for the Non-Invasive Assessment of Muscles) guidelines (SENIAM Project, 1999). The signal quality of each sensor was tested and sensor placement repeated if necessary and re-evaluated. Additionally, the EMG of the subjects' maximal voluntary isometric contraction (MVIC) of each muscle was measured before the experiment.



Indices	Muscle name
	Upper leg
GT	Gluteus maximus muscle
RF	Rectus femoris muscle
BF	Biceps femoris muscle
ST	Semitendinosus muscle
VL	Lateral vastus muscle
VM	Medial vastus muscle
	Lower leg
GL	Lateral gastrocnemius muscle
GM	Medial gastrocnemius muscle
SL	Soleus muscle
TA	Tibialis anterior muscle

Figure 3.3: *Overview of selected mono- and biarticular leg muscles (modified with permission from Kjpargeter (2017a, 2017b)). Indices and muscle names are explained on the right.*

3.2.3. Data processing

The instants of perturbation release were manually identified from the recorded video-sequences and appropriate events were set in the motion tracking system. In the following, data were processed (and analyzed) using MATLAB software (R2014a, The Math-Works, Inc., Natick, MA, USA).

EMG data were filtered first with second-order Butterworth low-pass (200 Hz) and high-pass (10 Hz) filters, then full-wave rectified, and finally a one-second moving average filter was applied. This process was also applied to the MVIC measurements. The processed EMGs of each muscle were normalized to the peak value of the processed MVIC (Halaki & Ginn, 2012). Moreover, instants of time during the phases IP, PP and RP were manually selected. The instant of time during the RP was set to 0.25 s after the instant of perturbation release (see above). To determine the change in muscle activity, we calculated differences in EMG values (dEMG) from

[3] In the result section, the leg muscles of the left and right leg are distinguished by indices additions: L for the left leg, R for the right leg.

the instants of time during IP and the corresponding PP phase. Subject means from the dEMG were calculated for each experimental condition.

Kinetic and kinematic data were filtered using a Butterworth filter (4th order and 25 Hz cutoff frequency) and grand means (from all subjects) were calculated. Due to incomplete data, some trials had to be removed from the analysis.

The orientation of the GRF vector (in the sagittal plane) with respect to the horizontal axis was calculated from the kinetic data. Simplified virtual two-dimensional models were calculated from the kinematic data: a one-segmented virtual model (from ankle to shoulder) to evaluate the overall body orientation in the sagittal plane (termed the body angle); and a two-segmented model (leg: ankle to hip and head-arms-trunk: hip to shoulder) to evaluate the leg orientation (termed *leg angle*) and the hip angle illustrated by stick figures in Figure 3.9.

3.2.4. Statistical comparison

Based on the conceptual model (Rode & Seyfarth, 2013), the changes of leg muscle activity in response to external perturbations (increasing, non-changing or decreasing EMG values) and different experimental conditions were predicted for the selected muscles (Figure 3.3). To evaluate the predictions, the dEMG values were statistically tested. To this end, Gaussian nonlinear mixed-effect (NLME) models were used for repeated measurements per subject, using the NLME package of the statistics software *R* (RStudio Inc., 2015, Version 0.99.486). Furthermore, a no-intercept model was compared with an intercept-only model using likelihood ratio tests to identify significances in the EMG differences. Effects of load (perturbation forces), leg configuration (knee angles) and combinations of both were considered. Detailed information, such as the source code developed in R-Studio (Annex 1) and its output (Annex 2), as well as results (f- and p-values) from the analysis of variances (ANOVA) can be found in the annex.

The different statistical NLME models (M1 – M5) are designed to investigate the following hypotheses:

M1) The dEMG changes when any external perturbation is introduced.

M2) The perturbation force has a linear effect on the dEMG.

M3) The knee angle has a linear effect on the dEMG.

M4) The knee angle affects EMG differences presuming that a linear force effect (*M2*) exists.

M5) The slope of the (presumed) linear force effect is systematically affected by the knee angle.

The NLME models compare the mean dEMG (differences in EMG between IP and PP phase) of all the subjects for the different experimental conditions. The NLME models increase in complexity when the variables of perturbation force (different pulling forces) and leg configuration (different initial knee angles) are included. Each NLME model results in an

intercept value y indicating whether muscle activity increases (positive values) or decreases (negative values).

E.M1) $y = \beta_0,$

with β_0 being the linear equation representing the mean difference between unperturbed and perturbed EMG values.

E.M2) $y = \beta_0 + \beta_1 * force,$

with β_0 being the linear equation and $\beta_1 * force$ representing the influence from the different perturbation forces with a linear relationship to the different perturbation (pulling) forces.

E.M3) $y = \begin{cases} \beta_0 \\ \beta_0 + \beta_1, \\ \beta_0 + \beta_2 \end{cases}$

with β_0 being the linear equation with respect to a specific leg configuration (here: 140°), and β_1 and β_2 representing the other knee angles. Here, linearity need not be assumed.

E.M4) $y = \begin{cases} \beta_0 + \beta_1 * force \\ \beta_0 + \beta_1 * force + \beta_2, \\ \beta_0 + \beta_1 * force + \beta_3 \end{cases}$ which leads to: $y = \begin{cases} \beta_0 + \beta_1 * force \\ (\beta_0 + \beta_2) + \beta_1 * force \\ (\beta_0 + \beta_3) + \beta_1 * force \end{cases}.$

Here, β_0 is the linear equation with respect to a specific leg configuration, $\beta_1 * force$ being the influence from the different perturbation forces, and β_2 and β_3 being the other leg configurations.

E.M5) $y = \begin{cases} \beta_0 + \beta_1 * force \\ (\beta_0 + \beta_2) + (\beta_1 * \beta_4) * force, \\ (\beta_0 + \beta_3) + (\beta_1 * \beta_5) * force \end{cases}$

with β_0 being the linear equation with respect to the different leg configuration β_{1-3}, considering the effect of different perturbation forces, and taking into account the fact that different knee angles $\beta_{4,5}$ might also affect the resulting muscle force.

3.3. Results

We analyzed changes in EMG over the grand mean of subjects for each muscle using statistical models (see Section 3.2.4). Considering 16 muscles and five different experimental conditions, 80 individual statistical analyses were conducted for each of the five different statistical models (M1 – M5). Among other aspects, the resulting data from the statistical analyses (Annex 2) included intercept values, which could be either positive (indicating increasing muscle activity) or negative (indicating decreasing muscle activity), and the corresponding levels of significance from the ANOVA. This allowed us to draw conclusions and to simplify the outcomes with respect to the different experimental conditions and statistical models (see Figure 3.4 – Figure 3.8 and Table 3.2 – Table 3.6); a few statistical models failed, so that no outcome was available for these cases. Assuming typical symmetry in muscle activation and to further simplify the figures, we only show the outcome for the left (stance) leg with respect to the experimental conditions (SA, SP and VD). The tables (Table 3.2 – Table 3.6) provide a more detailed overview of the outcome and additionally indicate the results from the ANOVA. In this way, we were able to directly compare the predicted and measured changes in EMG with respect to the different experimental conditions and statistical models. With reference to Table 3.2 – Table 3.6 we will use *matching cases* when predictions and statistical results correspond significantly, *cases with trends* when predictions and statistical results correspond without an appropriate significance level, and *mismatching cases* when predictions and statistical results do not correspond.

For our first goal (M1), we identified general responses of EMG to the different external perturbations. Except for the SP condition, most biarticular muscles responded with significantly increasing or decreasing EMG (Table 3.2, Exp). In contrast to biarticular muscles, monoarticular muscles showed similar activation under all experimental conditions. Responses were mostly significant, i.e. muscle activity either increased or decreased, although some responses could not be identified due to failed statistical analyses. With respect to horizontal perturbations (i.e. the experimental conditions AA, AP, SA, SP), the mono- and biarticular muscles (Figure 3.4 and Table 3.2) corresponded to the predictions in 49 out of 64 cases (~77 %). However, more predictions were confirmed for biarticular than for monoarticular muscles (28 vs. 21). Including the cases with trends, most predictions of the biarticular muscles were confirmed in the experimental conditions. In contrast, the monoarticular muscles did not display such a consistent outcome. In response to the VD condition, the outcome of the biarticular muscles as well as the monoarticular shank muscles did not fulfill the predictions. However, the monoarticular knee extensor muscles (VM, VL) in both legs were in line with the predictions for the VD condition.

In M2, we quantified whether the perturbation force had a linear effect on EMG activity in response to the different experimental conditions. In this context, most biarticular muscles showed significant changes in EMG in response to horizontal perturbations (AA, AP, SA, SP), whereas only few monoarticular muscles showed significantly increasing EMG (Table 3.3, Exp). However, with respect to vertical perturbations (VD condition) mono- and biarticular muscle EMG mostly did not change or in fact decreased. Compared to the conceptual model (Figure 3.5 and Table 3.3), mono- and biarticular muscles confirmed the predictions in 56 out of 80 (~70 %) cases (including nine cases with trends). Similar to M1, biarticular muscles showed more matching cases than monoarticular muscles. With respect to the biarticular muscles, 75 % of the predictions (30 out of 40) were confirmed. The total number of matching cases (including

monoarticular muscles) was highest in M1, which also holds true when cases with trends are included. The mismatching cases were distributed over all the experimental conditions and were not condition-specific.

In M3, it was quantified whether the initial leg configuration (i.e., the different knee angles) had a linear effect on EMG differences. Considering all the experimental conditions, the different leg configurations did affect the biarticular muscles in the SA condition, but only selectively with respect to the other experimental conditions (Table 3.4, Exp). In contrast, monoarticular muscles showed more significant changes of EMG in the SA, SP, and VD condition. Including the cases with trends, the outcomes of M3 (Figure 3.6 and Table 3.4) were mostly in line with the predictions although the total number of matching cases was lower than in M1 or M2. Furthermore, the number of missing outcomes due to failed statistical models was higher. Consequently, the number of cases with trends increased (19). However, statistical analyses resulted in only five mismatching cases, which were not focused on any particular experimental condition. In contrast to the previous analyses, results for monoarticular muscles in VD consistently confirmed the predictions.

In M4, we investigated the effects of different leg configurations, given a linear effect of the perturbation force, on muscle activity. In this context, the most significant EMG changes of biarticular muscles were observed in the SA condition (7 of 8 muscles), whereas only up to four muscles showed significant changes in EMG in response to the other experimental conditions (Table 3.5, Exp). Compared with this, the largest effects in the monoarticular muscles were observed in the SP and VD condition. However, a few muscles were affected in the other conditions. Out of a maximum of 80 cases, the outcome (Figure 3.7 and Table 3.5) included 40 matching cases, 13 cases with trends, and 9 mismatching cases. Interestingly, mismatching cases in VD were only assigned to muscles located medially in the legs (LGM, LVM and RVM), which was also observed in M2. Similar to previous observations, the vastii muscles of the left leg did not conform to the predictions in the AP condition and the AA condition. In contrast to the previous models, left hamstrings (LBF, LST) did not correspond to the predictions for the SA condition.

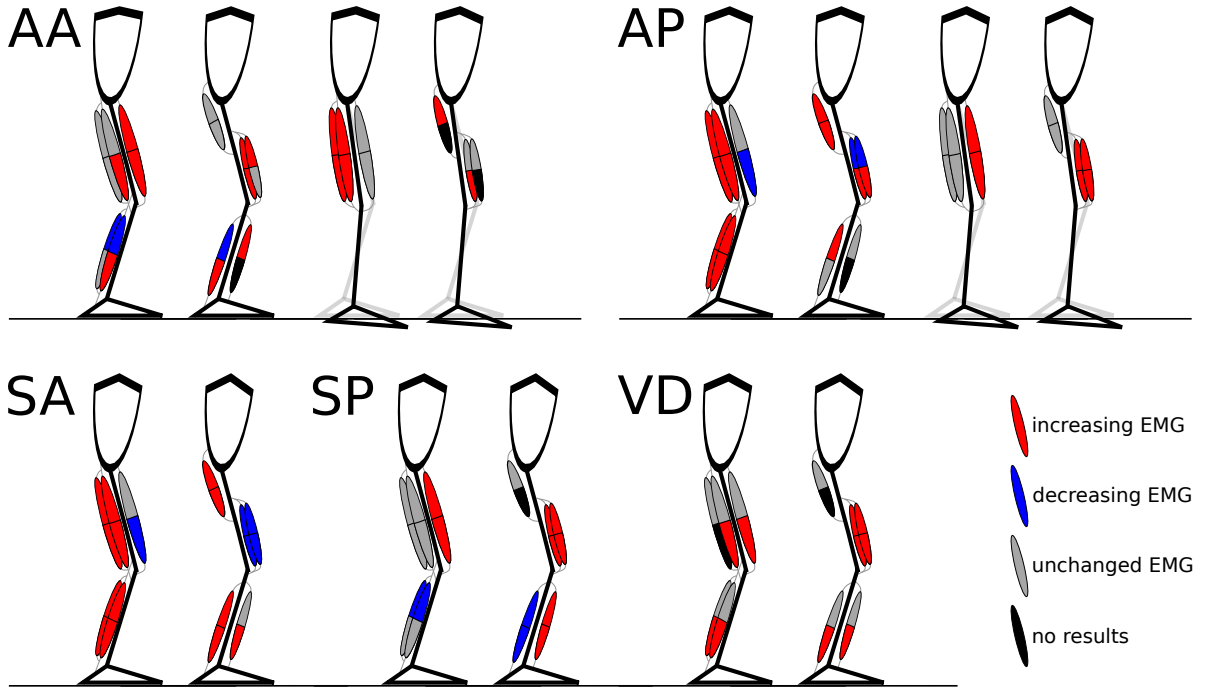


Figure 3.4: *Outcomes of the statistical comparison for M1 with respect to the different experimental conditions (AA: ankle-anterior, AP: ankle-posterior, SA: shoulder-anterior, SP: shoulder-posterior and VD: vertical direction). Two diagrams always form a pair showing results for mono- (right) and biarticular (left) muscles. In AA and AP, the results are divided between the stance leg (left pair) and the swing leg (right pair). The colored top half of the muscle diagrams shows the predicted change in EMG and the lower half shows the experimental outcomes.*

Table 3.2: *Results are given of the statistical analysis for M1 of mono- and biarticular muscles with predictions (Mod) and experimental results (Exp). Numbers indicate changes in EMG: +1 = significant increase, ±0 = no significant change, -1 = significant decrease; three dashes indicate that no data were available. The level of significance is shown by asterisks: * indicates p-value < 0.05 and ** indicates p-value < 0.02. Bold digits indicate matching cases, italic digits indicate cases with trends, mismatching cases are indicated in brackets.*

Biarticular muscles									
Conf.		**RRF**	**LRF**	**LGL**	**LGM**	**LST**	**RST**	**LBF**	**RBF**
AA	*Mod*	0	+1	-1	-1	0	+1	0	+1
	Exp	**+0**	**+1****	*-0*	(+1*)	**-1****	**+1****	**+0**	**+1****
AP	*Mod*	+1	0	+1	+1	+1	0	+1	0
	Exp	**1****	**-1****	**+1****	**+1****	**+1****	**-0**	**+1****	**-0**
SA	*Mod*	0	0	+1	+1	+1	+1	+1	+1
	Exp	**-1***	**-1***	**+1****	**+1****	**+1****	**+1****	**+1****	**+1****
SP	*Mod*	+1	+1	-1	-1	0	0	0	0
	Exp	**+1****	**+1****	*-0*	*-0*	**+0**	**-0**	**-0**	**-1***
VD	*Mod*	0	0	0	0	0	0	0	0
	Exp	---	(+1**)	(+1**)	(+1**)	(+1*)	---	---	---
Monoarticular muscles									
Conf.		**LGT**	**RGT**	**LSL**	**LTA**	**LVM**	**LVL**	**RVM**	**RVL**
AA	*Mod*	0	+1	-1	+1	+1	+1	0	0
	Exp	**+0**	---	(+1*)	---	*+0*	**+1****	(+1**)	---
AP	*Mod*	+1	0	+1	0	-1	-1	+1	+1
	Exp	**+1****	**+0**	*+0*	---	(+1**)	(+1**)	**+1****	**+1****
SA	*Mod*	+1	+1	+1	0	-1	-1	-1	-1
	Exp	**+1****	---	**+1****	(+1*)	**-1****	**-1****	**-1****	**-1****
SP	*Mod*	0	0	-1	+1	+1	+1	+1	+1
	Exp	---	---	**-1***	**+1****	**+1****	**+1****	**+1****	**+1****
VD	*Mod*	0	0	0	0	+1	+1	+1	+1
	Exp	---	---	(+1**)	(+1**)	**+1****	**+1****	**+1****	---

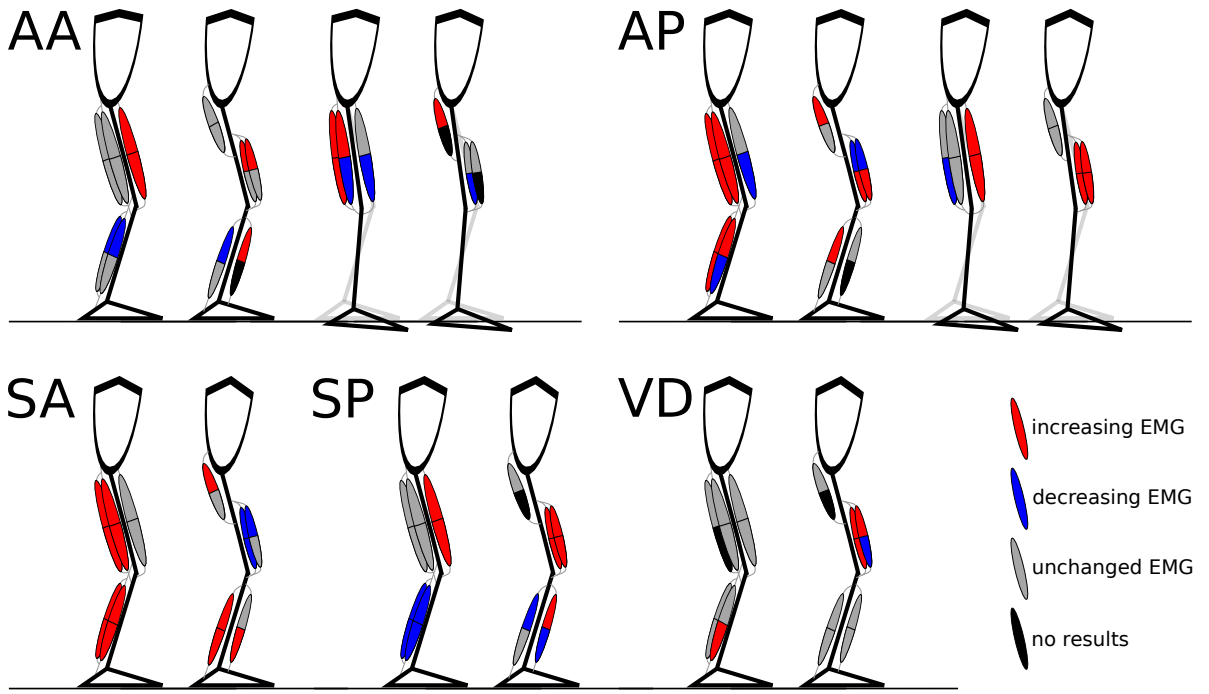


Figure 3.5: *Outcomes of the statistical comparison for M2 with respect to the different experimental conditions (AA: ankle-anterior, AP: ankle-posterior, SA: shoulder-anterior, SP: shoulder-posterior and VD: vertical direction). Two diagrams always form a pair showing results for mono- (right) and biarticular (left) muscles. In AA and AP, the results are divided between the stance leg (left pair) and the swing leg (right pair). The colored top half of the muscle diagram shows the predicted change in EMG and the lower half shows the experimental outcomes.*

Table 3.3: *Results are given of the statistical analysis for M2 of mono- and biarticular muscles with predictions (Mod) and experimental results (Exp). Numbers indicate changes in EMG: +1 = significant increase, ±0 = no significant change, -1 = significant decrease; three dashes indicate that no data were available. The level of significance is shown by asterisks: * indicates p-value < 0.05 and ** indicates p-value < 0.02. Bold digits indicate matching cases, italic digits indicate cases with trends, mismatching cases are indicated in brackets.*

***Biarticular* muscles**									
Conf.		***RRF***	***LRF***	***LGL***	***LGM***	***LST***	***RST***	***LBF***	***RBF***
AA	*Mod*	0	+1	-1	-1	0	+1	0	+1
	Exp	**-1****	**+1****	*-0*	*+0*	**-0**	**+1****	**+0**	(-1**)
AP	*Mod*	+1	0	+1	+1	+1	0	+1	0
	Exp	**+1****	**-1***	**+1****	(-1**)	**+1****	**-1****	**+1****	**-0**
SA	*Mod*	0	0	+1	+1	+1	+1	+1	+1
	Exp	**-1****	**-0**	**+1****	**+1****	**+1****	**+1****	**+1****	*+0*
SP	*Mod*	+1	+1	-1	-1	0	0	0	0
	Exp	**+1****	**+1****	**-1****	**-1****	**-0**	**-1****	**-0**	**-0**
VD	*Mod*	0	0	0	0	0	0	0	0
	Exp	---	**+0**	**+0**	(+1**)	+0	---	---	---
***Monoarticular* muscles**									
Conf.		***LGT***	***RGT***	***LSL***	***LTA***	***LVM***	***LVL***	***RVM***	***RVL***
AA	*Mod*	0	+1	-1	+1	+1	+1	0	0
	Exp	**-0**	---	*+0*	---	(-1*)	*+0*	**-1****	---
AP	*Mod*	+1	0	+1	0	-1	-1	+1	+1
	Exp	*+0*	**+0**	*+0*	---	(+1**)	(+1**)	**+1****	**+1****
SA	*Mod*	+1	+1	+1	0	-1	-1	-1	-1
	Exp	*+0*	---	**+1****	(+1**)	**-0**	**-1****	**-1****	**-1***
SP	*Mod*	0	0	-1	+1	+1	+1	+1	+1
	Exp	---	---	*-0*	(-1**)	**+1****	**+1****	**+1****	**+1****
VD	*Mod*	0	0	0	0	+1	+1	+1	+1
	Exp	---	---	**+0**	**+0**	(-1**)	**+1***	(-1**)	---

Results for M5, which evaluated whether the slope of the linear force effect is affected by the different leg configurations, displayed this effect only in a few mono- and biarticular muscles (Table 3.6, Exp). Interestingly, this time more mono- than biarticular muscles were affected and in addition predominantly in the SA and SP condition. Compared to the predictions from the conceptual model, the majority of the outcomes (Figure 3.8 and Table 3.6) were matching cases (34) and cases with trends (24) although, the number of cases with trends was higher than in the previous models, especially with respect to the biarticular muscles (13 in M5 vs. a mean of 6 in M1 – M4). In this way, the distribution of the outcomes between mono- and biarticular muscles was nearly balanced. In contrast to the other models, the number of mismatching cases was low (4).

In summary, the outcome of the statistical analyses predominantly verified the linear effects of different perturbation forces on EMG in comparison to effects due to different leg configurations; and mostly verified the predictions of the conceptual model. This is especially the case when cases with trends were also considered, thus providing evidence of the validity of the predictions. Except for M4, the results showed a reduced number of mismatching cases with increasing complexity, resulting in the lowest number in M5, although the number of cases with trends likewise rose.

Observed kinetic and kinematic (body angle, leg angle and hip angle; see Figure 3.9, stick figures on the left) parameters allow the reliability of the experimental design to be verified. The orientation of the parameters in space with respect to the horizontal direction for each experimental condition during the IP, PP and RP phases is shown in Figure 3.9. Similar to the analysis of EMG (see Section 3.2.4), parameter differences from PP to the IP phase were calculated (Figure 3.10). The orientation in space of the virtual body (Figure 3.9, 1) was below 90° (relative to the ground) during all phases of the measurement, which holds true for all experimental conditions. Thus, the body leaned slightly forward and did not change much during the whole measurement period. Furthermore, the kinematic data show that the (virtual) leg angles were similar to the virtual body thus supporting the fact that subjects did not change their posture, although measured differences (IP vs. PP phase) in the orientation of the leg angle (Figure 3.10, 2) were higher compared to the virtual body. The changes in the leg angle are positive in response to perturbations in the anterior direction and negative in response to perturbations in the posterior direction. Observed changes in the hip angle (Figure 3.10, 3) are very small and are not in line with the response pattern of the leg angle.

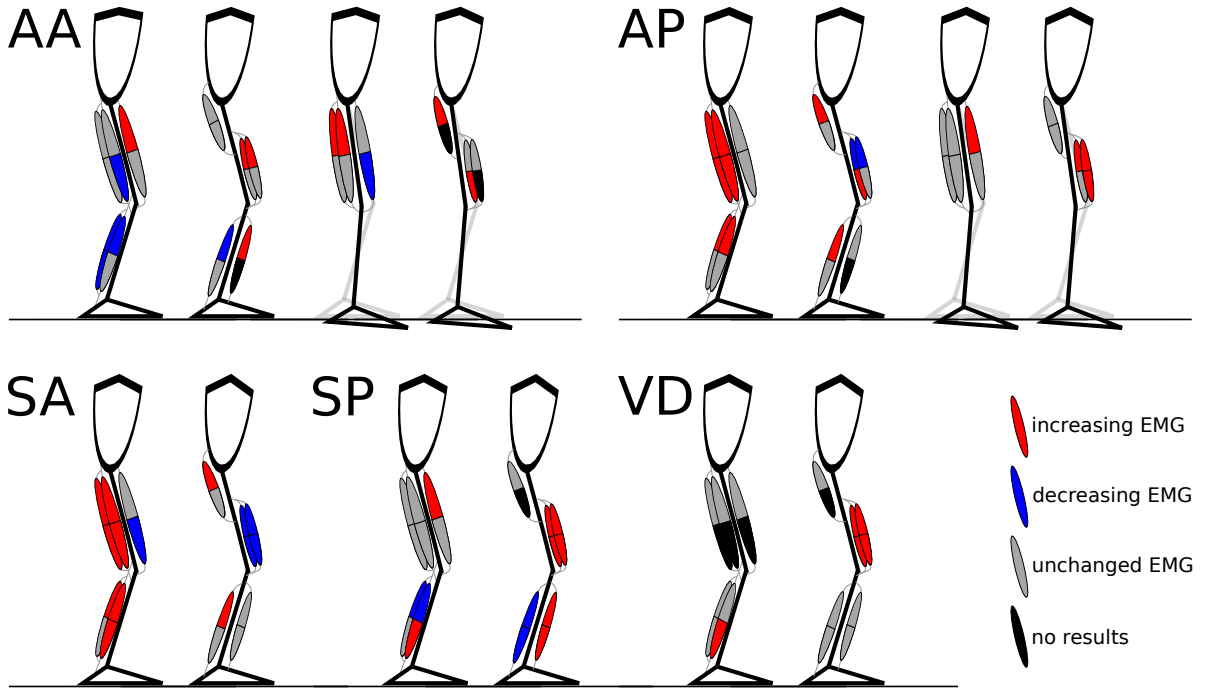


Figure 3.6: *Outcomes of the statistical comparison for M3 with respect to the different experimental conditions (AA: ankle-anterior, AP: ankle-posterior, SA: shoulder-anterior, SP: shoulder-posterior and VD: vertical-direction). Two diagrams always form a pair showing results for mono- (right) and biarticular (left) muscles. In AA and AP, the results are divided between the stance leg (left pair) and the swing leg (right pair). The colored top half of the muscle diagram shows the predicted change in EMG and the lower half shows the experimental outcomes.*

Table 3.4: *Results are given of the statistical analysis for M3 of mono- and biarticular muscles with predictions (Mod) and experimental results (Exp). Numbers indicate changes in EMG: +1 = significant increase, ±0 = no significant change, -1 = significant decrease; three dashes indicate that no data were available. The level of significance is shown by asterisks: * indicates p-value < 0.05 and ** indicates p-value < 0.02. Bold digits indicate matching cases, italic digits indicate cases with trends, mismatching cases are indicated in brackets.*

***Biarticular* muscles**									
Conf		***RRF***	***LRF***	***LGL***	***LGM***	***LST***	***RST***	***LBF***	***RBF***
AA	*Mod*	0	+1	-1	-1	0	+1	0	+1
	Exp	**-1***	*+0*	**-1***	*+0*	**-1***	*+0*	**+0**	*+0*
AP	*Mod*	+1	0	+1	+1	+1	0	+1	0
	Exp	*+0*	**-0**	*+0*	*+0*	**+1****	**-0**	**+1****	**-0**
SA	*Mod*	0	0	+1	+1	+1	+1	+1	+1
	Exp	**-1****	**-1****	*+0*	**+1****	**+1****	**+1****	**+1****	**+1****
SP	*Mod*	+1	+1	-1	-1	0	0	0	0
	Exp	**+1****	*+0*	*-0*	(+1**)	**+0**	**-1***	**+0**	**-0**
VD	*Mod*	0	0	0	0	0	0	0	0
	Exp	---	---	+0	(+1**)	---	---	---	---
***Monoarticular* muscles**									
Conf		***LGT***	***RGT***	***LSL***	***LTA***	***LVM***	***LVL***	***RVM***	***RVL***
AA	*Mod*	0	+1	-1	+1	+1	+1	0	0
	Exp	**+0**	---	*+0*	---	(-0)	*+0*	(+1*)	---
AP	*Mod*	+1	0	+1	0	-1	-1	+1	+1
	Exp	*+0*	**+0**	*+0*	---	*+0*	(+1*)	*+0*	**+1***
SA	*Mod*	+1	+1	+1	0	-1	-1	-1	-1
	Exp	*+0*	---	*+0*	**+0**	**-1****	**-1****	**-1****	**-1***
SP	*Mod*	0	0	-1	+1	+1	+1	+1	+1
	Exp	---	---	**-1***	**+1****	**+1****	**+1****	*+0*	**+1****
VD	*Mod*	0	0	0	0	+1	+1	+1	+1
	Exp	---	---	**+0**	**+0**	**+1****	**+1****	**+1****	---

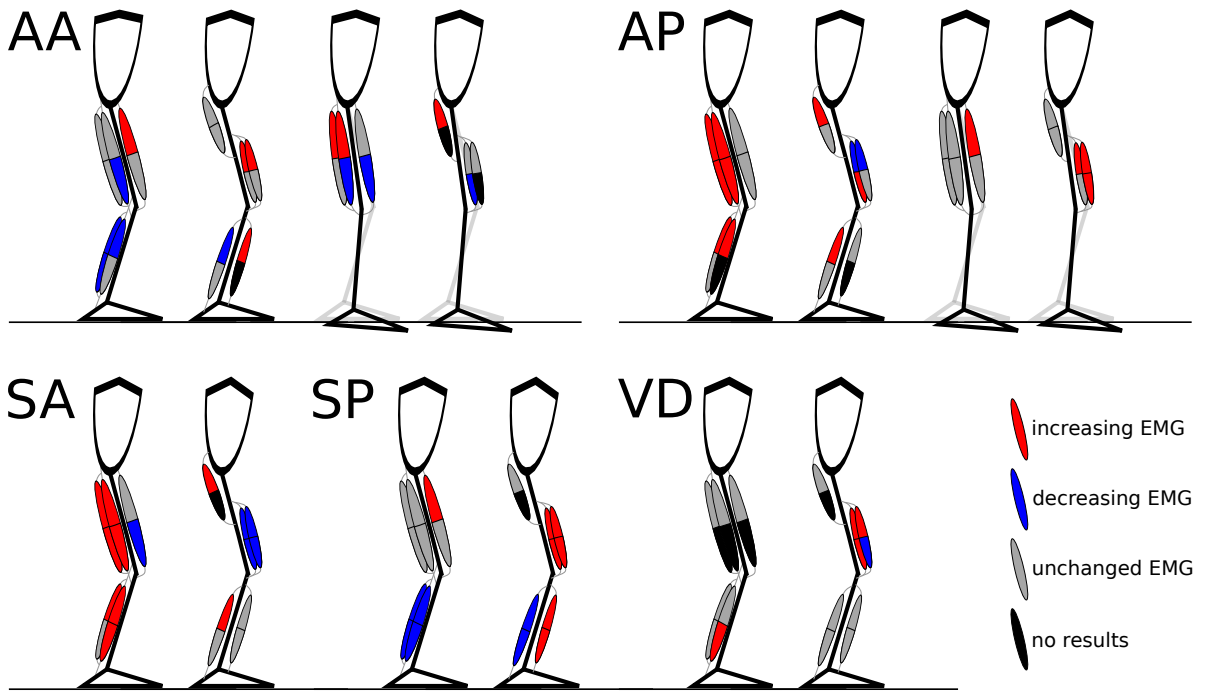


Figure 3.7: *Outcomes of the statistical comparison for M4 with respect to the different experimental conditions (AA: ankle-anterior, AP: ankle-posterior, SA: shoulder-anterior, SP: shoulder-posterior and VD: vertical-direction). Two diagrams always form a pair showing results for mono- (right) and biarticular (left) muscles. In AA and AP, the results are divided between the stance leg (left pair) and the swing leg (right pair). The colored top half of the muscle diagram shows the predicted change in EMG and the lower half shows the experimental outcomes.*

Table 3.5: *Results are given of the statistical analysis for M4 of mono- and biarticular muscles with predictions (Mod) and experimental results (Exp). Numbers indicate changes in EMG: +1 = significant increase, ±0 = no significant change, -1 = significant decrease; three dashes indicate that no data were available. The level of significance is shown by asterisks: * indicates p-value < 0.05 and ** indicates p-value < 0.02. Bold digits indicate matching cases, italic digits indicate cases with trends, mismatching cases are indicated in brackets.*

Biarticular muscles									
Conf		***RRF***	***LRF***	***LGL***	***LGM***	***LST***	***RST***	***LBF***	***RBF***
AA	*Mod*	0	+1	-1	-1	0	+1	0	+1
	Exp	**-1***	*+0*	**-1***	*+0*	**-1***	*+0*	**+0**	(-1*)
AP	*Mod*	+1	0	+1	+1	+1	0	+1	0
	Exp	*+0*	**-0**	*+0*	---	**+1****	**-0**	**+1****	**-0**
SA	*Mod*	0	0	+1	+1	+1	+1	+1	+1
	Exp	**-1****	**-1****	*+0*	**+1****	(-1**)	**+1****	(-1**)	**+1****
SP	*Mod*	+1	+1	-1	-1	0	0	0	0
	Exp	**+1****	*+0*	**-1***	**-1****	**-0**	**-1***	**-0**	**-0**
VD	*Mod*	0	0	0	0	0	0	0	0
	Exp	---	---	**+0**	(+1**)	---	---	---	---
Monoarticular muscles									
Conf		***LGT***	***RGT***	***LSL***	***LTA***	***LVM***	***LVL***	***RVM***	***RVL***
AA	*Mod*	0	+1	-1	+1	+1	+1	0	0
	Exp	**-0**	---	*+0*	---	(-0)	(-0)	**-1***	---
AP	*Mod*	+1	0	+1	0	-1	-1	+1	+1
	Exp	*+0*	**+0**	*+0*	---	*+0*	(+1*)	*+0*	**+1***
SA	*Mod*	+1	+1	+1	0	-1	-1	-1	-1
	Exp	---	---	*+0*	**+0**	**-1****	**-1****	**-0**	**-0**
SP	*Mod*	0	0	-1	+1	+1	+1	+1	+1
	Exp	---	---	**-1***	**+1****	**+1****	**+1****	**+1****	**+1****
VD	*Mod*	0	0	0	0	+1	+1	+1	+1
	Exp	---	---	**+0**	**+0**	(-1**)	**+1****	(-1*)	---

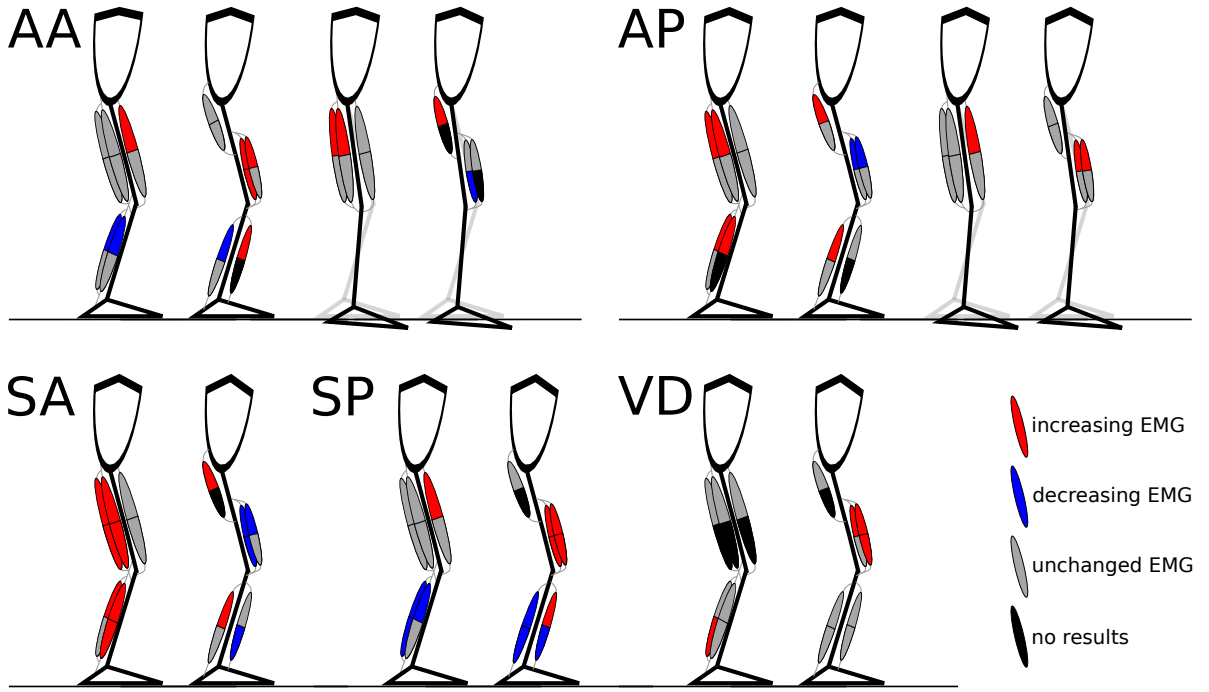


Figure 3.8: *Outcomes of the statistical comparison for M5 with respect to the different experimental conditions (AA: ankle-anterior, AP: ankle-posterior, SA: shoulder-anterior, SP: shoulder-posterior and VD: vertical-direction). Two diagrams always form a pair showing results for mono- (right) and biarticular (left) muscles. In AA and AP, the results are divided between the stance leg (left pair) and the swing leg (right pair). The colored top half of the muscle diagram shows the predicted change in EMG and the lower half the experimental outcomes.*

Table 3.6: *Results are given of the statistical analysis for M5 of mono- and biarticular muscles with predictions (Mod) and experimental results (Exp). Numbers indicate changes in EMG: +1 = significant increase, ±0 = no significant change, -1 = significant decrease; three dashes indicate that no data were available. The level of significance is shown by asterisks: * indicates p-value < 0.05 and ** indicates p-value < 0.02. Bold digits indicate matching cases, italic digits indicate cases with trends, mismatching cases are indicated in brackets.*

Biarticular muscles									
Conf		***RRF***	***LRF***	***LGL***	***LGM***	***LST***	***RST***	***LBF***	***RBF***
AA	*Mod*	0	+1	-1	-1	0	+1	0	+1
	Exp	**-0**	*+0*	*-0*	*+0*	**-0**	*+0*	**+0**	(-0)
AP	*Mod*	+1	0	+1	+1	+1	0	+1	0
	Exp	*+0*	**-0**	*+0*	---	*+0*	**-0**	*+0*	**-0**
SA	*Mod*	0	0	+1	+1	+1	+1	+1	+1
	Exp	**-0**	**-0**	*+0*	**+1***	**+1****	*+0*	**+1***	*+0*
SP	*Mod*	+1	+1	-1	-1	0	0	0	0
	Exp	**+1****	*+0*	**-1****	*-0*	**-0**	**-0**	**-0**	**-0**
VD	*Mod*	0	0	0	0	0	0	0	0
	Exp	---	---	(+1**)	**+0**	---	---	---	---
Monoarticular muscles									
Conf		***LGT***	***RGT***	***LSL***	***LTA***	***LVM***	***LVL***	***RVM***	***RVL***
AA	*Mod*	0	+1	-1	+1	+1	+1	0	0
	Exp	**+0**	---	*+0*	---	(-0)	**+1***	**-1***	---
AP	*Mod*	+1	0	+1	0	-1	-1	+1	+1
	Exp	*+0*	**+0**	*+0*	---	**+0**	*+0*	*+0*	*+0*
SA	*Mod*	+1	+1	+1	0	-1	-1	-1	-1
	Exp	---	---	*+0*	**-1***	**-0**	**-1***	**-1****	**-0**
SP	*Mod*	0	0	-1	+1	+1	+1	+1	+1
	Exp	---	---	**-1***	(-1**)	**+1***	**+1****	*+0*	*+0*
VD	*Mod*	0	0	0	0	+1	+1	+1	+1
	Exp	---	---	**+0**	**+0**	**+1****	*+0*	*+0*	---

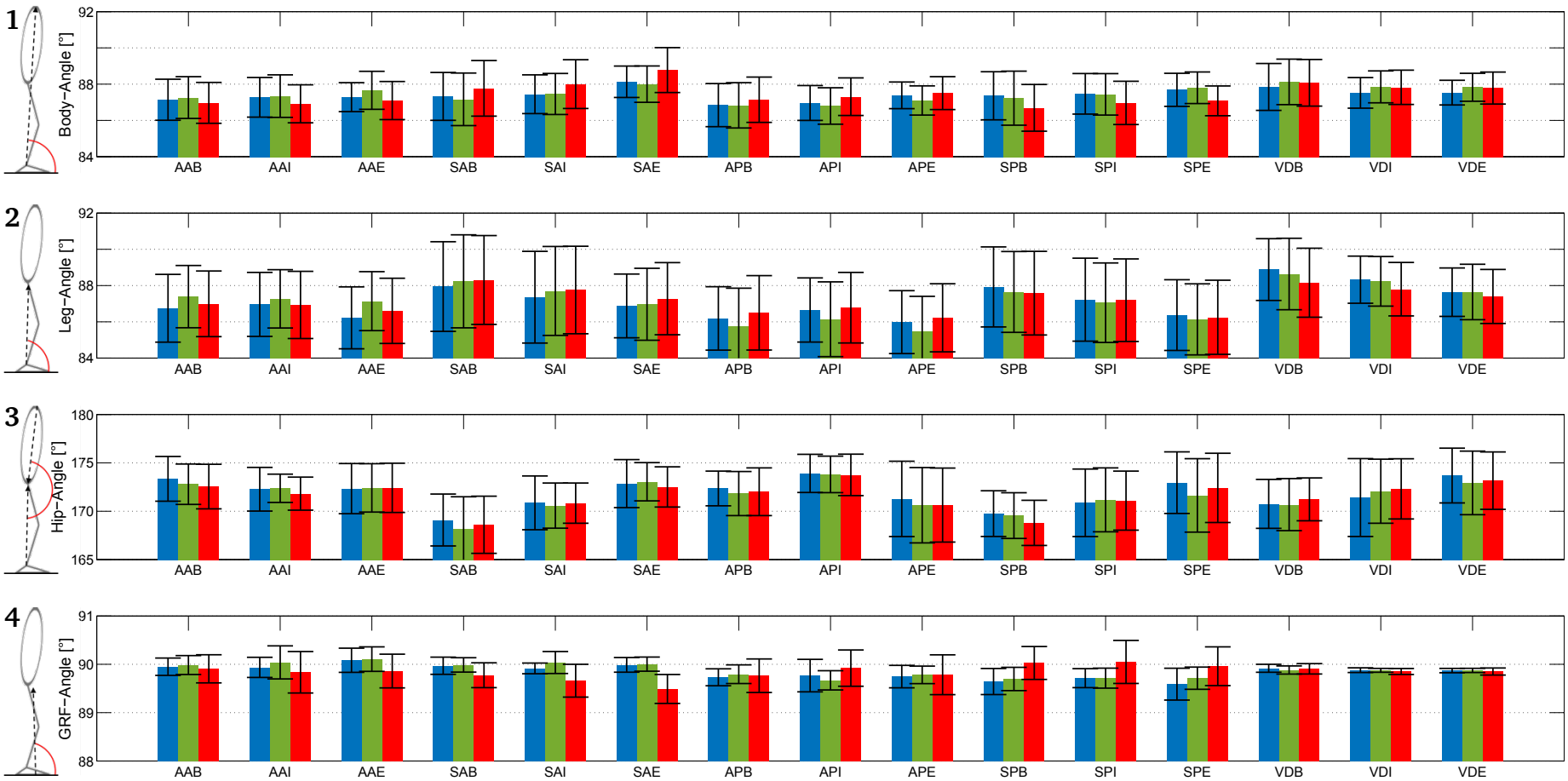


Figure 3.9: *Grand mean of kinematic parameters with respect to experimental conditions. Kinematic parameters include the orientation of the virtual body (1), the virtual leg (2), and the GRF (4); furthermore, the hip angle (3) is also given. Stick figures on the left illustrate the calculated angles (indicated in red). With respect to the stick figures, orientation in space (only 1, 2 and 4) is defined as follows: 0° in forward direction, 90° in upward direction and 180° backwards. Colored bars represent parameter values for the IP (blue), PP (green) and RP (red) phase during each experimental condition, furthermore the standard deviation (black error bar) is also shown. The first two letters of the abbreviations on the x-axis refer to the different experimental conditions (AA, AP, SA, SP, and VD) and the last letter indicates the different leg configurations (B = bent, I = intermediate, E = extended).*

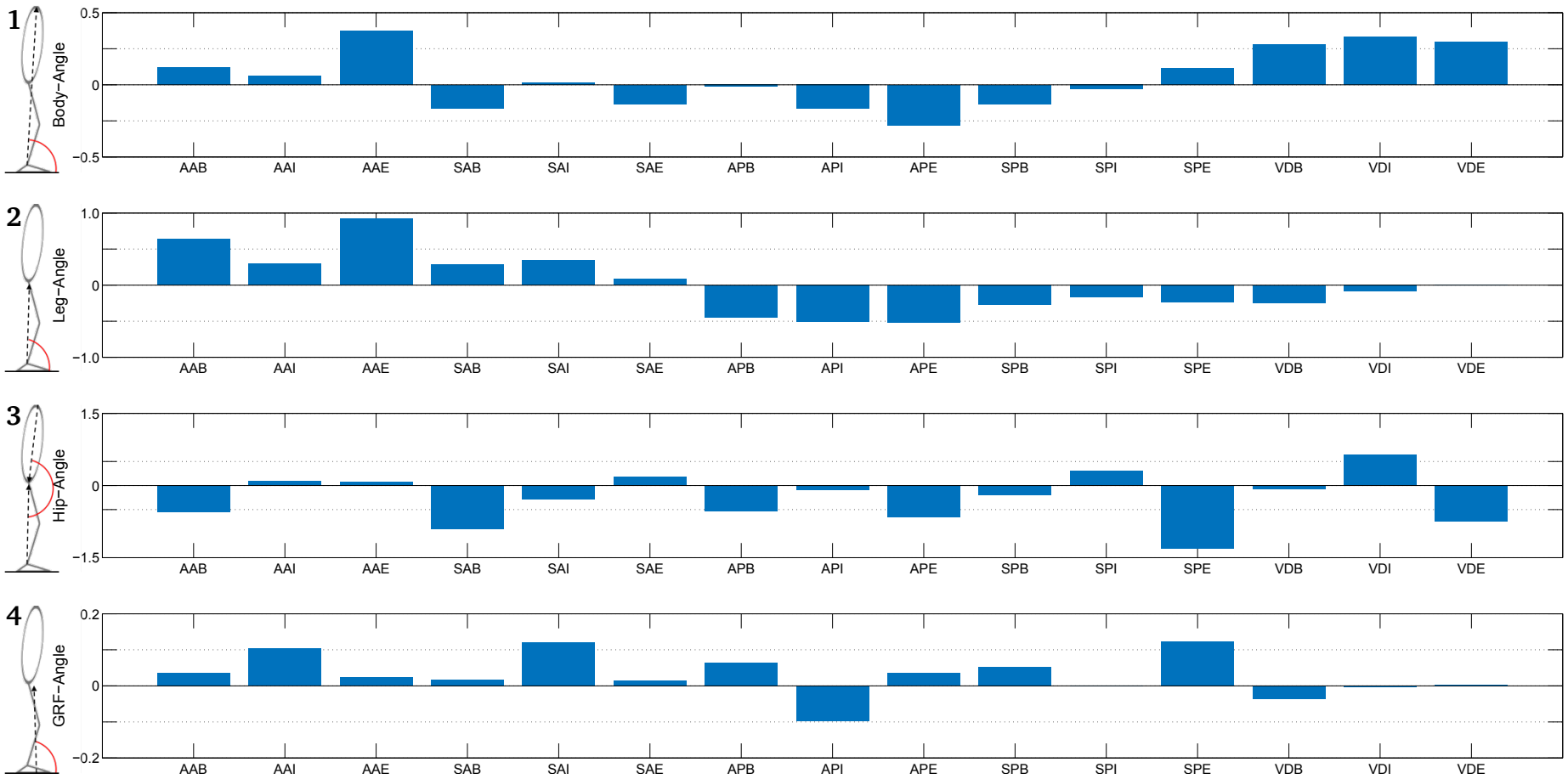


Figure 3.10: *Differences in the kinematic parameters from PP to IP phase (green bars minus blue bars in Figure 3.9) with respect to the experimental conditions. Kinematic parameters include the orientation of the virtual body (1), the virtual leg (2) and the GRF (4); furthermore, the hip angle (3) is also given. Stick figures on the left illustrate the calculated angles (indicated in red). The first two letters of the abbreviations on the x-axis refer to the different experimental conditions (AA, AP, SA, SP, and VD) and the last letter indicates the different leg configurations (B = bent, I = intermediate, E = extended).*

3.4. Discussion

In this study, we investigated the response of mono- and biarticular muscles of the human leg to quasi-static horizontal perturbations (constant pulls at shoulder and ankle level) during upright standing. Based on a conceptual model (Rode & Seyfarth, 2013), we predicted changes in the EMG of mono- and biarticular muscles in response to the introduced perturbations. We hypothesized quasi-linear relationships between the introduced perturbation force, leg configuration (knee angle) and corresponding changes in EMG activation of selected muscles, which was in line with predictions based on the conceptual model. Our results suggest that an upright posture can be maintained by manipulating the GRF via perpendicular leg forces that are mainly created by biarticular leg muscles. Not only is the EMG modulated in relation to perturbation strength or leg configuration but also in relation to a combination of both.

The outcomes of the different statistical models (M1 – M5) give insights into the individual responses of selected muscles during horizontal and vertical perturbations. The results indicate that mainly biarticular muscles respond to the horizontal perturbations in order to maintain an upright posture, which is in line with previous findings (Doorenbosch et al., 1995; Doorenbosch & van Ingen Schenau, 1995; Hof, 2001; Jacobs & van Ingen Schenau, 1992) suggesting the capacity of biarticular muscles for redirecting GRF in the horizontal direction. Similar to the identified muscle synergies counteracting horizontal ground translations (Chvatal & Ting, 2013) thus causing whole body sway, in the present study mono- and biarticular muscles respond with increasing or decreasing EMG (Figure 3.4, Table 3.2, SA and SP condition). However, muscle synergies have not been identified and this remains for further data analyses. Finally, the outcome of the statistical model M2 show that changes in EMG are related to perturbation force; which is line with similar findings on postural feedback gains (Kim, Atkeson & Park, 2012; Park, Horak & Kuo, 2004). In addition, we compared experimental data with predictions from a conceptual model to further investigate its validity. Considering the number of matching cases and cases with trends in the mono- and biarticular muscles, the experimental outcome tends to comply with the predictions, also with respect to the different experimental conditions and statistical models.

With respect to the VD condition, the outcome of M1 (Figure 3.4, Table 3.2) shows that the EMG of biarticular muscles (LRF, LGL, LGM, LST) increased in response to the perturbations, which does not conform to the model predictions. In addition, the EMG of the monoarticular muscles LSL and LTA also unexpectedly increased. Interestingly, these muscles form antagonistic muscle groups in the thigh (LRF and LST) and the shank (LGL, LGM, LSL and LTA), respectively. This unexpected increase in EMG activity might be due to the experimental design. On the one hand, vertical loading is introduced to the arms, which pulls the trunk downwards around the shoulder causing trunk flexion. Here, the co-activation of LRF and LST might create counteractive torques to stabilize the hip and prevent the trunk from flexing. On the other hand, the experimental design includes different leg configurations that are not considered in M1. In contrast to the outcome of M1, which did not consider perturbation force and leg configuration, changes in the activity of mono- (LRF and LST) and biarticular muscles (LRF, LGL, LST), in M2 (Figure 3.5, Table 3.3) and M3 (Figure 3.6, Table 3.4), are in line with model predictions. This indicates that these muscles are co-activated in response to any perturbation in order to stabilize the knee angle, as suggested by Baratta et al. (1988) and Doorenbosch et al. (1995).The effect of the co-contraction of antagonistic muscles, which potentially reduces the mechanical reaction

and the EMG reaction to the sudden release of the quasi-static perturbation, is not considered in the conceptual model. However, also a combination of both effects from the experimental design and antagonistic co-contraction is feasible. The increase in EMG of the biarticular muscles might be evoked due to a (lateral) stiffening of the trunk, realized by rotational torques. Moreover, stiffening of the trunk (upper body) may also lead to stiffening of the legs (the lower body) to stabilize the whole (mechanical) system. No trunk muscles were investigated in this study to support this theory and the issue therefore remains open for future research.

Above we report that mismatching cases in M1 (VD condition) turned into matching cases, which was more prominent in M3 compared to the results of M2. Nevertheless, the outcome regarding the VD condition in M4 (investigating the effect of different knee angles under the condition of a linear force effect) still shows mismatches. Interestingly, both M2 and M4 show that only the medial muscles (LGM, LVM and RVM) did not match the predictions. For both of these cases LGM activity significantly increased, whereas LVM and RVM activity significantly decreased. This change in EMG may cause stiffening of the body in the frontal plane to prevent medio-lateral sway. Due to a lack of data (from failed statistical models) for all muscles, it remains unclear whether this observation holds true for medial hamstring muscles (LST and RST). However, future research may investigate whether this effect is observed in similar experimental or simulation studies.

In the experimental conditions AA and AP, perturbations were introduced at the right ankle, i.e. at the swing leg. The outcome of the knee extensor muscles (LVM, LVL) does not conform to the predictions from the model (see outcome of M1 – M4). This can result from the experimental design where we defined that subjects should maintain their swing limb at a fixed position next to the stance leg also during the PP phase when perturbations were introduced. Therefore, the necessary joint stability for the swing limb might be established by increased joint stability in the left stance leg, which, among other things, results from increased muscle activity in the monoarticular muscles of the left leg. Based on the kinematic chain, stiffer joints in the stance leg permit higher torques in the joints of the swing leg.

The orientation in space of the virtual body (Figure 3.9, 1) remained quite stable during all phases of the measurement and experimental conditions. In addition, merely very small differences emerged between the IP and PP phase in the hip angle (Figure 3.10, 3). Both indicate that the subjects successfully maintained their upright posture in spite of the introduced perturbations mainly by using their leg muscles and did not rely on trunk flexion and extension although the GRF vector was also almost vertical (Figure 3.9, 4). In view of the fact that the virtual body leaned forward (Figure 3.9, 1), the COM might have been shifted in the anterior direction. In this way and with the GRF pointing almost directly upwards, the COP must have been located in front of the ankle joints in order to facilitate the required joint torques to maintain an upright posture. This postural configuration is in line with Mergner (2012), who considers this posture essential for maintaining balance. However, the question remains open as to whether the small differences in GRF (Figure 3.10, 4) are caused by the relatively small perturbation forces compared to the subjects' body weight or simply normal body sway and is thus a side effect of the experimental design.

Although the orientation of the GRF (Figure 3.10, 4) did not show many changes throughout the experimental conditions, it might be interesting to further investigate GRF orientation with

respect to the largely ignored recovery phase. This phase is assumed to be more dynamic, due to the sudden release of the quasi-static perturbation force, and might provide further insights into the human balance recovery mechanism. Furthermore, it could also be interesting to further investigate the GRF orientation according to an approach described by Gruben and Boehm (2012), who identified different *posture-specific force intersection points* when hip and knee joints were rigid and both hip and knee torques were kept constant. This might help to further evaluate the outcomes of this study (with respect to M3) and, additionally, may improve our understanding of the influence of different leg configurations (different knee angles) on postural control in response to external perturbations.

There were several limitations to the present study. Producing forces by hand results in non-standardized perturbation procedures. Hence, the timing of the different experimental phases (IP, PP and RP) and pulling forces were not completely balanced within and between subjects. Computer-controlled devices to introduce perturbation might help to avoid these inaccuracies. Side effects such as co-activation of antagonistic muscle groups (in the VD condition) could be avoided by automatically (un)loading the body by quickly altering the ground level. This approach would result in a very similar design with respect to sequence (i.e. the different experimental phases: IP, PP, PP) and effect on the leg force (i.e. increase/drop and recovery due to the ground movement). Furthermore, real-time visualization of the knee and hip angle (e.g. by a digital goniometer) and swing leg position may help the subjects to better maintain the desired posture.

The study design allows further questions to be investigated. So far, the analyses have focused on the difference between initial (IP phase) and perturbation (PP phase) conditions. The quick release of the quasi-static perturbation leads to quite a dynamic response and may be considered as another perturbation that has to be coped with in order to recover the initial posture. In this context, advanced analyses of EMG would be interesting in order to evaluate the actual time muscles require to respond (to the perturbation) and relax (after the perturbation) and how this influences the recovery of the posture.

This study consolidates the relevance of the concept from Rode and Seyfarth (2013) for humans and improves the current understanding of how biarticular leg muscles contribute to upright human posture.

4. Leg mechanics in perturbed human hopping

4.1. Introduction

Understanding complex movements such as bipedal locomotion in biological systems is challenging. Simplified template models (Full & Koditschek, 1999) and mechanical models such as the spring-loaded inverted pendulum (SLIP) model (Blickhan, 1989) can help to improve our understanding of the underlying gait mechanisms. Research has shown that simplified biomechanical models can generate stable locomotion patterns for walking (Geyer, Seyfarth & Blickhan, 2006; Rummel et al., 2010; Wisse, Atkeson & Kloimwieder, 2005) or running (Seyfarth et al., 2003). Experimental studies have been used to identify gait parameters in relation to human data (Blum, Lipfert, Rummel & Seyfarth, 2010; Blum et al., 2009; Lipfert et al., 2014). However, the behaviors predicted by these simplified models are much less capable of coping with challenging conditions (e.g. challenging environments) compared to biological systems in terms of stability, flexibility and robustness.

Legged locomotion can be described as a composition of three locomotor sub-functions: elastic axial leg function (stance), rotational swing leg function (leg swinging) and body alignment (balancing/posture control) (Sharbafi & Seyfarth, 2017). Different combinations of these sub-functions result in gaits with different speeds and with specific gait properties (Sharbafi & Seyfarth, 2017). These sub-functions are interconnected by specific sensor-motor couplings, e.g. between axial leg force and rotational leg function (e.g. for postural balance), as described by the force modulated compliant hip (FMCH) model (Sharbafi & Seyfarth, 2015). Nevertheless, many of these interconnecting structures are not well understood (e.g. coupling between the two legs) and need to be investigated in future research.

Humans can easily cope with unexpected perturbations during locomotion through mechanical responses (e.g. from tendon elasticity) and motor control (e.g. muscle activation). Models show that sensory feedback (Geyer et al., 2003) as well as feedforward control (van der Krogt et al., 2009) are capable of modulating mechanical leg parameters (e.g. leg stiffness) for robust locomotion in the case of perturbations. Humans adapt leg stiffness in hopping and running in relation to surface stiffness (Farley et al., 1998; Ferris & Farley, 1997; Ferris et al., 1999, 1998; van der Krogt et al., 2009). The leg stiffens when the ground becomes softer, whereas the leg softens when the ground becomes stiffer (Farley et al., 1998; Ferris & Farley, 1997; Moritz & Farley, 2005; van der Krogt et al., 2009). In running, this adaptation of leg stiffness occurs during the first step on the changed ground surface (Ferris et al., 1999). However, the individual contributions of motor control and mechanical response in recovering from perturbations are not well quantified.

The goal of this study is to investigate how leg behavior (e.g. leg stiffness) is adjusted to recover from ground level perturbations during stance. This may help to describe and explain the response of the human body to sudden ground level perturbations. We expect that with the lowering of the ground level during the stance phase, the leg length becomes longer than in the unperturbed condition. This leads to a shortening of the leg extensor muscles (e.g. vastii at the knee joint). At the muscle-tendon system level, this results in a reduced tendon length and a reduced muscle and tendon force. The muscle response is expected to be delayed with respect to tendon dynamics due to the intrinsic velocity-dependent muscle properties

(force-velocity relationship, (Seyfarth, 2000, Chapter V)). As a result, both muscle length and eccentric muscle velocity will be reduced, which results both in reduced muscle force and also in reduced muscle stiffness (assuming that the muscle operates at the ascending limb of the force-length relationship, as expected in humans hopping at preferred hopping frequency). Hence, the response of the human body to a lowering in ground level is expected to result in a drop of leg force and leg stiffness based on the muscle-tendon dynamics of the leg extensor muscles. After the point of maximum ground dropping speed, the ground level is accelerated upward to slow down the downward movement until rest. During this phase, we expect the opposite response with increasing leg force and leg stiffness compared to the unperturbed condition.

4.2. Method

Ten subjects (8 male, 2 female) participated in an experimental study on perturbed hopping. Subjects were asked to hop on the spot at their individually preferred hopping frequency (PHF) and to continue hopping while a sudden vertical ground level perturbation was introduced during the stance phase.

Average subject characteristics are shown in Table 4.1. One subject had to be excluded from the data analysis due to inconsistencies during the measurement. The study was approved by the Ethics Committee of Technische Universität Darmstadt (in accordance with the Declaration of Helsinki) and written informed consent was provided by all subjects prior to the experiment. Subjects were given time for a warm up and to become familiarized with hopping barefoot on the perturbation platform. None of the participants reported any current cases of motor deficits.

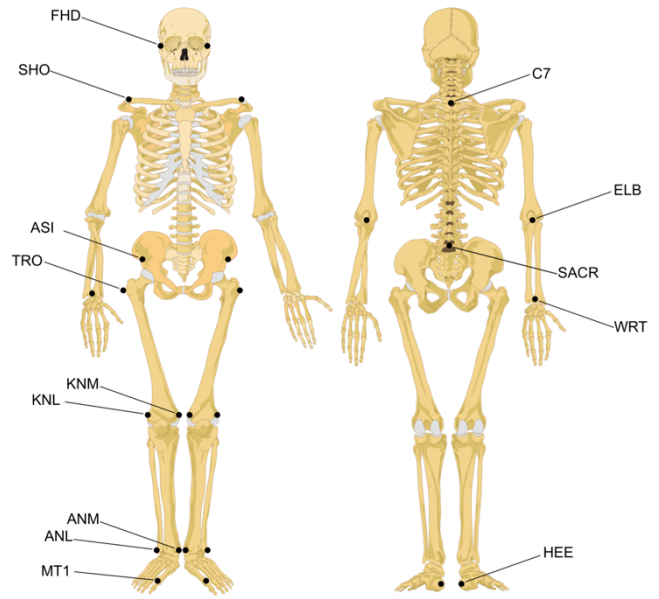
Table 4.1: *Subject characteristics, preferred hopping frequency (PHF) for each subject (#), the grand mean (∅) including standard deviation (±SD).*

#	age [yrs]	height [m]	mass [kg]	PHF	sex
1	26	1.63	61.60	2.28	M
2	25	1.73	66.15	2.27	F
3	27	1.86	77.52	2.58	M
4	25	1.67	61.54	2.16	F
5	24	1.84	94.76	2.56	M
6	24	1.80	81.88	2.08	M
7	24	1.78	71.48	2.64	M
8	33	1.79	65.55	2.50	M
9	26	1.67	66.51	2.25	M
∅	**26.00** *(± 1.78)*	**1.75** *(± 0.07)*	**71.80** *(± 8.56)*	**2.37** *(± 0.18)*	

4.2.1. Data collection

Three-dimensional (3D) whole body kinematics and ground reaction forces (GRF) were collected in this experiment.

Kinematic data were collected via 16 high-speed infrared cameras (Oqus 300 and 350+, Qualisys, Gothenburg, Sweden) with a sampling frequency of 250 Hz and were upsampled by linear interpolation to 1000 Hz for later analyses. The system was calibrated before measurements with each subject. The cameras recorded 3D positions of 26 reflective markers placed at anatomical landmarks spread over the whole body (Figure 4.1). Markers were attached to the skin using double-sided adhesive tape and were additionally secured with adhesive tape to assure good fixation regardless of sweat or impact vibrations.



Marker	Anatomical landmark
	Head & trunk
FHD	Temple[4]
C7	7th cervical vertebra
ASI	Anterior superior iliac spine
SACR	Sacrum spine
	Arms
SHO	Acromion
ELB	Olecranon
WRT	Wrist[5]
	Legs
TRO	Greater trochanter
KNL	Lateral epicondyle
KNM	Medial epicondyle
ANL	Lateral malleolus
ANM	Medial malleolus
	Feet
HEE	Calcaneus
MT1	1st metatarsal head

Figure 4.1: *Anatomical landmarks for marker placement. Markers are indicated by black dots on the human skeletons on the left (adapted from Clker-Free-Vector-Images (2017a, 2017b)). Indices and marker locations are specified on the right.*

4.2.2. Experimental procedure

Subjects were asked to hop steadily on the spot at their individually preferred hopping frequency for 15 s. After several hops (~7 s of measurement), a sudden ground level perturbation was introduced during the stance phase by a custom-made robotic perturbation platform. During the perturbation, the ground level dropped by 25, 50 or 75 mm (maximum speed: 1 m/s, acceleration: 7.85 m/s^2). Platform movements were triggered by force plate signals and were initiated when the vertical force magnitude exceeded 2.5 times the subject's

[4] Approximately in the region of the sphenoid bone (at the level between eye and ear).

[5] Undepressed skin surface point on the dorsal surface of the wrist midway between the radial and ulnar styloid processes (Reed, Manary & Schneider, 1999).

body weight (BW). The order of the perturbation height was randomized to avoid possible history-dependent (baseline) effects.

Subjects were instructed to return to steady-state hopping as quickly as possible after the perturbation and continue at this rate until the end of the measurement. Trials without any kind of perturbation were not conducted, hence subjects knew that a perturbation would occur while they were hopping.

4.2.3. Data processing

All data were processed and analyzed using custom software (MATLAB R2014a, The Math-Works, Inc., Natick, MA, USA).

In order to synchronize the kinematic and kinetic data, we hit the force plate with a tool (tagged with a reflective marker) after the start of the measurement but before subjects stepped on the platform. The corresponding peaks in force and acceleration were used to synchronize data for each trial. System calibration was conducted before each measurement. Therefore, and in order to align the origin of ordinates of the kinematic data to those of the force plate, we conducted subject-specific matrix translations and rotations. Vertical force (Fz) signals were appropriately corrected with respect to the inertial effects of the platform acceleration on the measured vertical ground reaction forces (GRF). Therefore, the inertia of the moveable platform multiplied by its acceleration was taken into account and the resulting inertial force was subtracted from the vertically measured force by the force plate. Kinetic and kinematic raw data were filtered using a 4th order low-pass Butterworth filter with 25 Hz cutoff frequency. From this data, the PHF for each trial was calculated for all successful hops by averaging cycle times for each subject.

Touchdown (TD) and take-off (TO) events were defined as the instant when the Fz magnitude exceeded or fell below 50 N, respectively. Vertical position data of the platform were derived twice to obtain platform accelerations. The sudden drop in acceleration (i.e. when the corresponding value fell below -0.04 m/s^2) defines the instant of perturbation initiation of the perturbed hop. The perturbed hop and the four preceding hops were taken into account for the analyses. Signals of the stance phases were linearly interpolated to 100 time-equidistant time steps.

We manually screened for suspicious trials. First, we checked the perturbation profiles (i.e. the platform position over time during the movement) and excluded outliers with respect to the timing of movement initiation. Second, we compared Fz of the perturbed hops and excluded trials that clearly differed from the subjects' Fz mean within the first 40 % of stance time.

Finally, 118 trials were included in the analyses, which resulted in an average of 4.38 trials per subject and perturbation height. In total, 39 perturbed and 156 unperturbed (four per trial) hops for each perturbation height have been analyzed. From this, individual means were calculated which were then used to calculate an inter-individual grand mean for each perturbation height.

4.2.4. Center of mass, dynamic leg length

Coordinates of the segmental center of mass as well as of the whole body center of mass (COM) were calculated from the observed kinematic data using the method of Winter (2009). In addition, COM trajectories were optimized according to a method introduced by Maus, Seyfarth and Grimmer (2011) based on kinetic and kinematic data. During contact, dynamic leg length (l_{Leg}) was defined as the distance between COM and center of pressure (COP). COP data were derived from the force-plate recordings using vertical force signals (Winter, 2009). Leg length and Fz were normalized to each subject's total height and body weight, respectively.

4.2.5. Quasi-leg stiffness, inverse dynamics, coefficient of elasticity

Quasi-leg stiffness

Firstly, we calculated the effective leg stiffness as described in Blum et al. (2009). Here, a linear force-length relationship is presumed. The leg stiffness is given by:

$$k = \frac{F_{max}}{\Delta L} \text{ [E1]},$$

with F_{max} being the maximum vertical force (Fz) and ΔL the amount of leg compression Δl_{Leg}. Leg compression is defined as:

$$\Delta l_{Leg}(t) = l_0 - l_{Leg}(t) \text{ [E2]},$$

with l_0 being the leg length measured one frame before TD and $l_{Leg}(t)$ the leg length during the stance phase.

Secondly, we calculated the dynamic leg stiffness, i.e. stiffness of the effective leg for each instant of the stance phase. Dynamic leg stiffness is defined as:

$$kLeg(\text{t}) = \frac{GRFz(t)}{\Delta l_{Leg}(t)} \text{ [E3]}.$$

Furthermore, we calculated the derivatives $\dot{\text{F}}\text{z}$ and $\dot{k}Leg$ of Fz and $kLeg$, respectively.

Inverse dynamics

As subjects hopped with both feet on one force plate, we could not separate the leg forces of the two limbs. Hence, we consider a virtual leg (similar to the effective leg described in the sections above) that represents the behavior of both legs. We normalized virtual leg length to subjects' total height. From this, we calculated the two-dimensional (2D) inverse dynamics (in the sagittal plane) following the method of Winter (2009) and recommendations from Günther, Sholukha, Kessler, Wank and Blickhan (2003) considering translational and rotational joint accelerations.

Coefficient of elasticity

Additionally, we calculated the coefficient of elasticity (CEL) according to Geyer et al. (2003):

$$CEL = \left(1 - \frac{A}{A_{max}}\right)^2 \text{ [E4]},$$

with A being the area enclosed by the leg force-leg length trace of the effective leg and A_{max} the total area covered by the enclosing rectangle with the area $F_{max} * \Delta L$.

4.3. Results

Results for the different perturbation heights and corresponding kinematics and kinetic responses are presented in the following sections. The data and curves represent the grand mean of 9 subjects. Data for the unperturbed hops and perturbed are denoted and indicated differently by name and different color in accordance with the corresponding perturbation heights: REF and blue indicate unperturbed hopping, P25 and light red for perturbations of 25 mm, P50 and intermediate red for perturbations of 50 mm, and P75 and dark red for perturbations of 75 mm.

The biomechanical characteristics for the grand mean of the subjects were investigated with respect to unperturbed hopping and the different perturbation conditions (see Table 4.2). The hopping patterns were similar to previous studies on human hopping on the spot, e.g. comparing characteristics such as average PHF, stance time and peak vertical GRF (Farley & Morgenroth, 1999; Ferris & Farley, 1997; Funase et al., 2001; Hobara et al., 2010; Riese, Seyfarth & Grimmer, 2013).

The subject's response to perturbed ground level was characterized by two subsequent phases: 1) the beginning of negative acceleration of the platform during stance, (at 30 % stance) and 2) the positive acceleration of the platform (i.e. when the downward platform movement is slowed down) after the instant of platform acceleration reversal (P25 – 58 %, P50 – 65 % and P75 – 76 %). In the following sections, these events are presented either by vertical grey bars (Figure 4.2, Figure 4.3, Figure 4.5, Figure 4.6 and Figure 4.7) or black diamonds and triangles (Figure 4.4 and Figure 4.9), respectively.

4.3.1. Leg kinematics and kinetics

Measured Fz and $\dot{F}z$ curves for unperturbed and perturbed hopping are presented in Figure 4.2 and Figure 4.3, respectively. In comparison to unperturbed hopping, under perturbed conditions Fz shows smaller force peaks. Furthermore, force values decrease earlier and faster compared to the unperturbed condition; additionally, stance time decreases with increasing ground level perturbation height.

In the early stance phase (first 30 % of contact), force development of the perturbed hops is similar to unperturbed hops. Furthermore, Fz of unperturbed and perturbed hopping shows an increasing slope during this period. This effect is reflected in the time series $\dot{F}z$ (Figure 4.3), which shows two subsequent rising phases of the signal during this period. From perturbation initiation (after 1st grey bar), Fz and $\dot{F}z$ curves of all conditions are still very similar in shape.

At around 36 % of stance time, the platform movement starts (i.e. the ground drops). Simultaneously, perturbed Fz and $\dot{F}z$ curves separate from the unperturbed condition and show an earlier and much faster descent with time. As long as the platform acceleration is downward (36 – 58 %), tracings of perturbed Fz and $\dot{F}z$ signals remain similar, irrespective of perturbation height.

Once the platform acceleration is reversed, i.e. the downward platform movement is slowed down by positive upward acceleration, differences in Fz and $\dot{F}z$ between the perturbed conditions become visible. This event is different for each perturbation height: P25 – 58 %, P50 – 65 %, P75 – 76 % (Figure 4.2 and Figure 4.3, grey bars). Starting at this instant, $\dot{F}z$ signals of perturbed conditions begin to rise. Compared to the unperturbed condition, these ascending traces start earlier (depending on the perturbation height) and are less steady. Nevertheless, $\dot{F}z$ of all conditions is at a very similar level at TO.

Table 4.2: *Means (and standard deviation) of selected variables for the grand mean for the different hopping conditions. NORM values refer to the unperturbed hops (mean of 4 hops before the perturbation). Fz_{max} refers to the peak of Fz, ΔLL_{max} refers to the peak of leg compression Δl_{Leg}, k_{max} refers to the peak of kLeg, k_{rising} represents leg stiffness during the phase of leg compression (from TD until ΔLL_{max}), $k_{falling}$ represents leg stiffness during the phase of leg extension (from ΔLL_{max} until TO). Furthermore, peak values of ankle, knee and hip flexion angle (A-, K-, H-Angle) and joint torques (A-, K-, H-Torque) are given.*

Variable	NORM	P25	P50	P75
Stance time [ms]	264.76 (27.01)	268.8 (24.04)	259.46 (32.94)	247.24 (31.05)
Fz_{max} *[N/BW]*	3.0343 (0.0699)	2.9343 (0.3167)	2.9937 (0.355)	2.9499 (0.3730)
ΔLL_{max} *[m]*	0.0602 (0.008)	0.0576 (0.0101)	0.0572 (0.0122)	0.0581 (0.0125)
k_{max}	50.4916 (1.4453)	52.4928 (8.1126)	54.1851 (9.9082)	52.8002 (10.8351)
k_{rising}	51.0522 (1.4914)	52.9571 (9.5701)	54.6589 (10.0683)	53.2407 (11.0070)
$k_{falling}$	48.1274 (1.9096)	50.8674 (8.1126)	49.4959 (7.1141)	48.2748 (7.5479)
CEL	0.9153 *(.0215)*	0.8657 *(0.0757)*	0.8274 *(0.0707)*	0.8448 *(0.0638)*
A-angle [°]	82.8812 *(5.8803)*	84.9053 *(6.3796)*	83.6468 *(5.3705)*	82.7362 *(5.8621)*
K-angle [°]	134.82 *(6.9572)*	135.6548 *(7.3988)*	135.5473 *(5.7969)*	234.3297 *(6.3341)*
H-angle [°]	107.5401 *(8.3747)*	107.8812 *(8.0589)*	107.9374 *(7.6938)*	107.1421 *(8.2531)*
*A-torque [Nm/(BW*LL)]*	0.3092 *(0.1139)*	0.2870 *(0.1080)*	0.3429 *(0.1322)*	0.3212 *(0.1157)*
*K-torque [Nm/(BW*LL)]*	0.300 *(0.1371)*	0.2945 *(0.1282)*	0.2449 *(0.1304)*	0.2758 *(0.1170)*
*H-torque [Nm/(BW*LL)]*	0.1081 *(0.0751)*	0.1069 *(0.0680)*	0.1659 *(0.0942)*	0.1408 *(0.0550)*

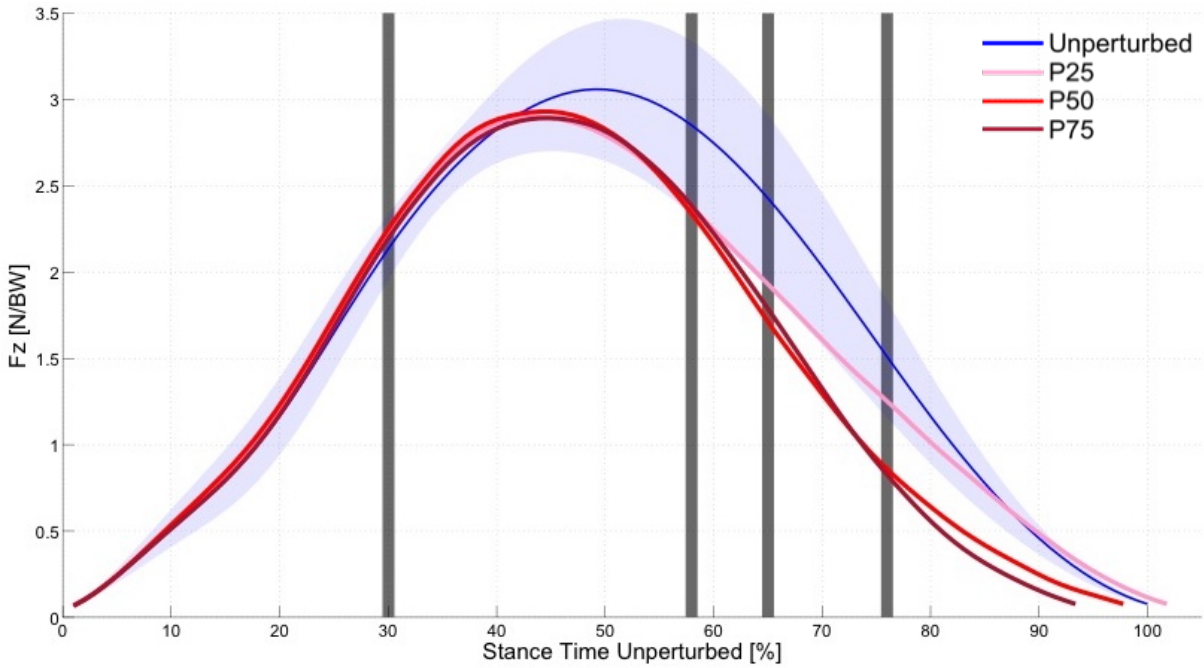


Figure 4.2: *Grand mean of the vertical GRF (Fz) for the different hopping conditions. The blue line represents unperturbed hopping; additionally, the corresponding standard deviation (light blue area) is shown. Lines of different shades of red indicate different perturbation heights. Vertical grey bars indicate (from left to right) the instant of perturbation and the instants of platform vertical acceleration reversal.*

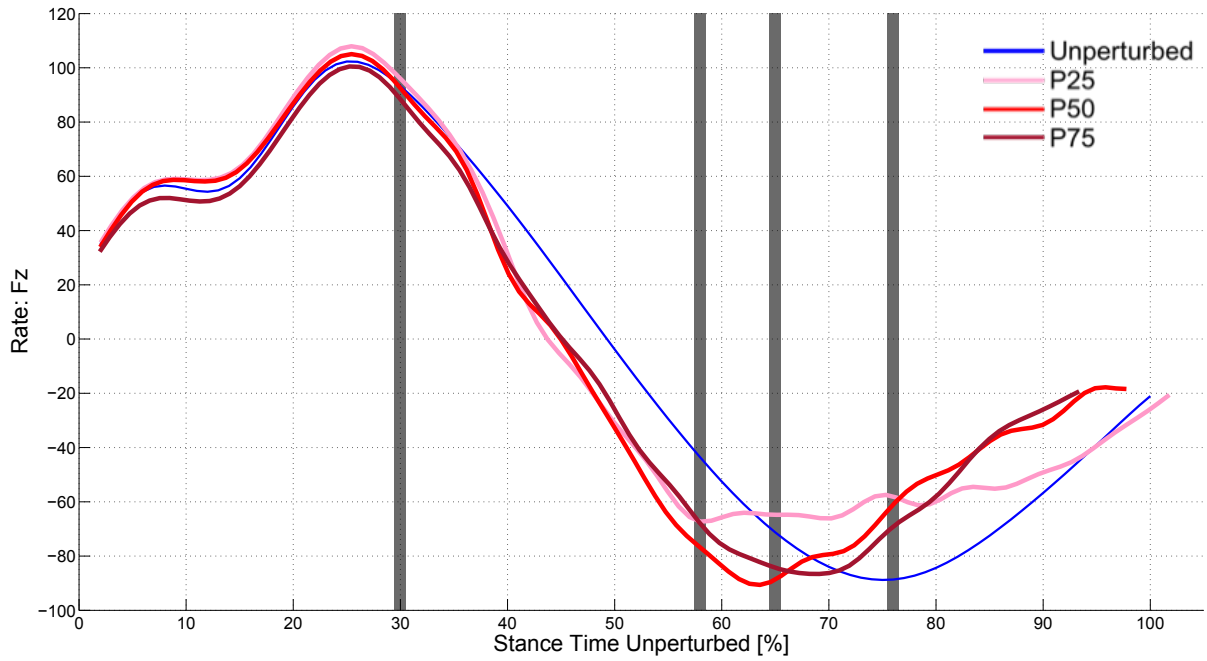


Figure 4.3: *Derivative $\dot{F}z$ of vertical GRF (Fz) for unperturbed (blue line) and perturbed (red lines) hopping. Different perturbation heights are indicated by different shades of red. Vertical grey bars indicate (from left to right) the instant of perturbation and the instants of acceleration reversal.*

While hopping without ground level perturbations, the force-length (FL) relation (Figure 4.4, blue lines) shows a close-to-spring-like shape. Until the instant of perturbation initiation (indicated by black diamonds), the traces of perturbed hopping (red lines) and unperturbed hopping (blue line) are very similar. Afterwards, the traces start to differ and while the peak values of force and leg compression are lower during perturbed hopping compared to the unperturbed case. Until the instant of acceleration reversion (indicated by black triangles), the FL traces of perturbed hopping are similar to the traces of unperturbed hopping. From that point on until the end of the investigation, perturbed traces differ again from unperturbed hopping traces. Nevertheless, perturbed FL traces show a common trend with only one intersection point. With respect to individual shapes, the FL trace of P75 is most similar to the FL curve of unperturbed hopping (Figure 4.4, C). It seems that the enclosed area of the FL work loops (indicating change in mechanical system energy) as well as the total area stretching from the peak points of the traces (with respect to the vertical zero line) decrease with increasing perturbation height. Nevertheless, they are larger than in unperturbed hopping. These observations are supported by the coefficients of elasticity (CEL) (see Section 4.2.5). The CEL values for different perturbation conditions are given in Table 4.2. It is shown that the CEL is lower for perturbed hopping than for unperturbed hopping. Indeed, only differences between unperturbed hopping and P50 or P75 are significant.

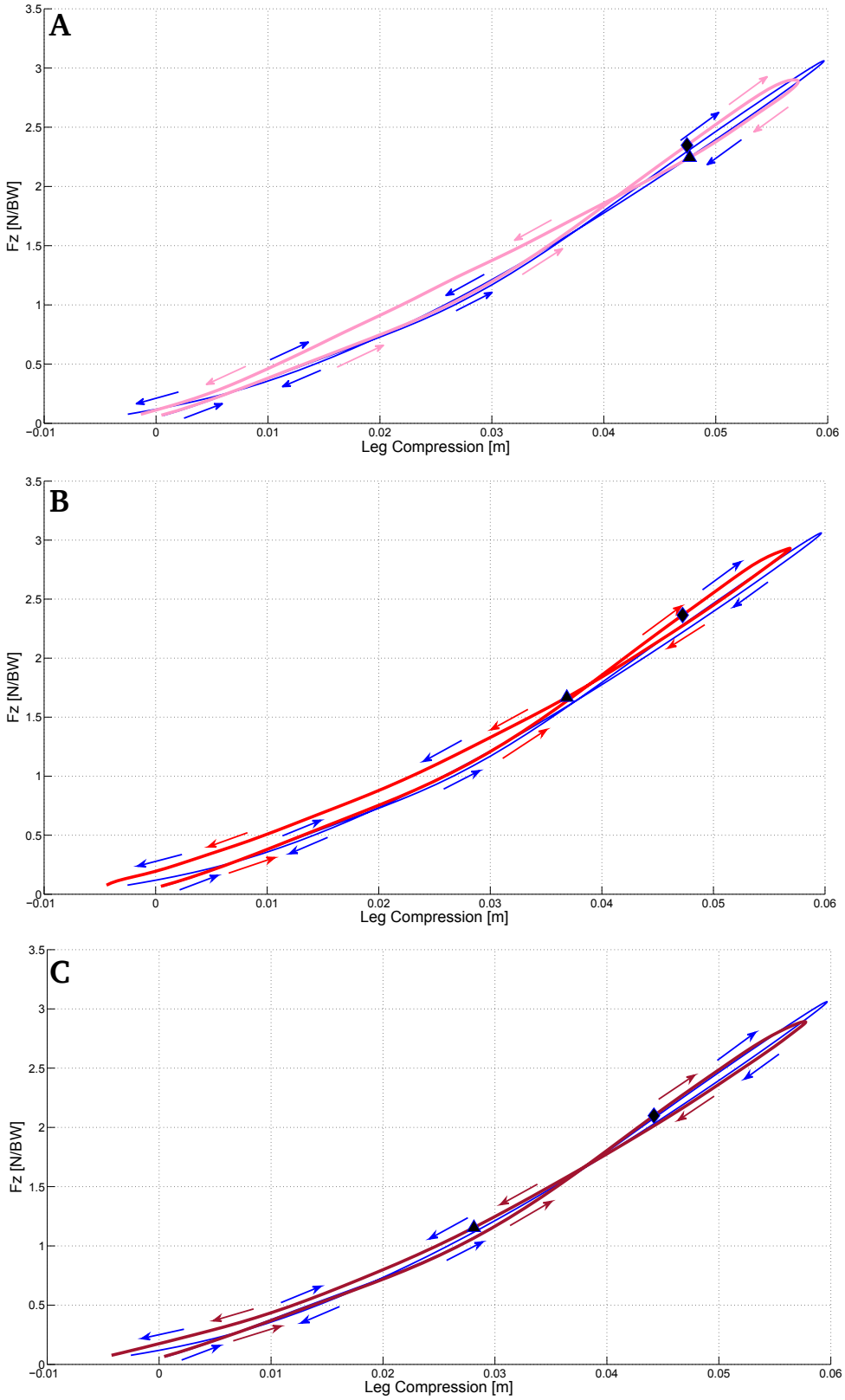


Figure 4.4: *Mean traces of the force-length relationships of the effective leg. Blue lines: grand means of unperturbed hopping. A-C: Different perturbations (P25, P50, P75), indicated by lines of different shades of red. Black diamonds indicate the instant when platform acceleration begins. Black triangles indicate the instant of acceleration reversal.*

4.3.2. Leg characteristics

Leg characteristics comprising dynamic stiffness *kLeg* (Section 4.2.5) of the effective leg and its derivative $\dot{k}Leg$ are shown in Figure 4.5 and Figure 4.6.

In general, *kLeg* traces of unperturbed hopping (Figure 4.5, blue lines) increase in the first half and decrease in the second half of the stance phase. The corresponding negative slope of the stiffness rate (Figure 4.6, blue line) is similar to the development of Fz (described in Section 4.3.1). Until the instant of perturbation initiation, $\dot{k}Leg$ traces (Figure 4.6, red lines) of perturbed and unperturbed hopping show a similar progression including the curvature (increasing slope) at the beginning, which is more prominent compared to Fz. Afterwards, traces of perturbed hopping are distinguished from the trace of unperturbed hopping indicating an adaptation to the perturbation. The subjects' response to ground level perturbations during stance is characterized by two subsequent phases: 1) the negative acceleration of the platform and 2) the positive acceleration of the platform after the instant of acceleration reversal. In Figure 4.5, leg stiffness differences between unperturbed hopping (blue line) and perturbed hopping (red line) are present at around 36 % of stance time when the movement of the platform starts. While the trace of unperturbed hopping (Figure 4.5, blue line) decreases constantly, the traces of perturbed hopping decrease earlier and faster. Irrespective of perturbation height, the perturbed *kLeg* traces differ from the unperturbed case in a similar manner until the instant of acceleration reversal (first phase). In the second phase, *kLeg* adapts depending on the perturbation height: the traces decrease much more slowly than in the unperturbed condition and show small oscillations. These observations are more pronounced with respect to $\dot{k}Leg$ (Figure 4.6). Here, the perturbed $\dot{k}Leg$ traces suddenly drop at the beginning of platform movement. This shift in $\dot{k}Leg$ remains at about the same level until the instant of acceleration reversal. With the beginning of upward platform acceleration, the $\dot{k}Leg$ traces suddenly increase and may even exceed the $\dot{k}Leg$ of unperturbed hopping.

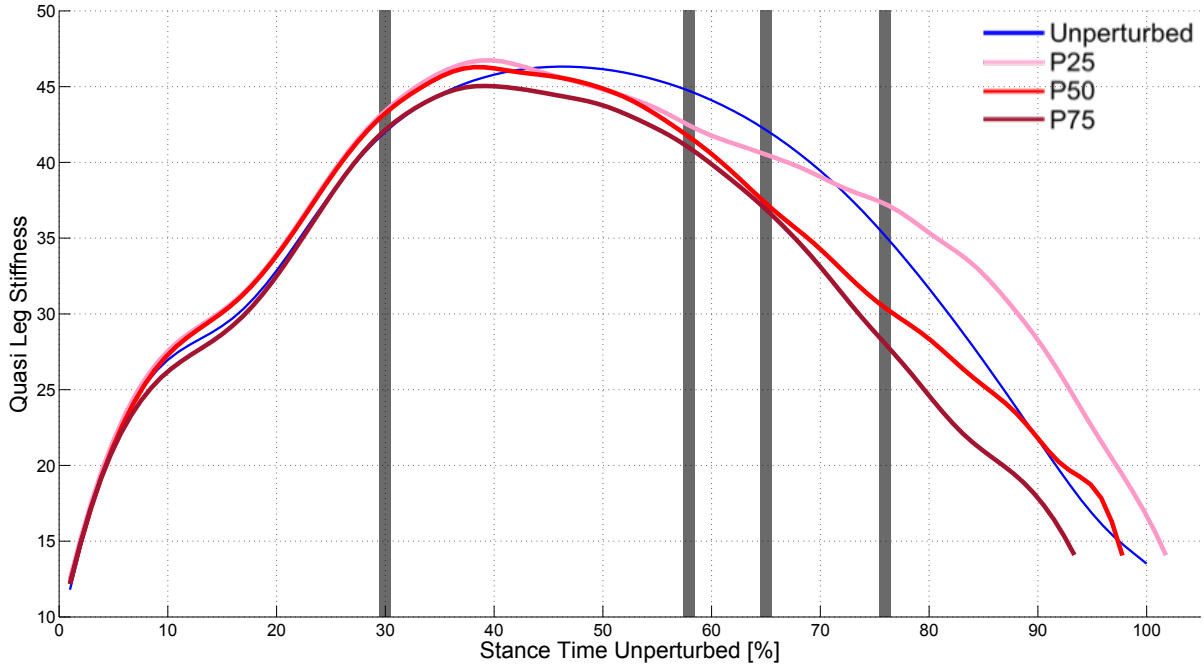


Figure 4.5: *Grand mean of leg stiffness kLeg for unperturbed (blue line) and perturbed (red lines) hops. Different perturbation heights are indicated by different shades of red. Vertical grey bars indicate (from left to right) the instant of perturbation initiation and the perturbation-height-dependent instants of acceleration reversal.*

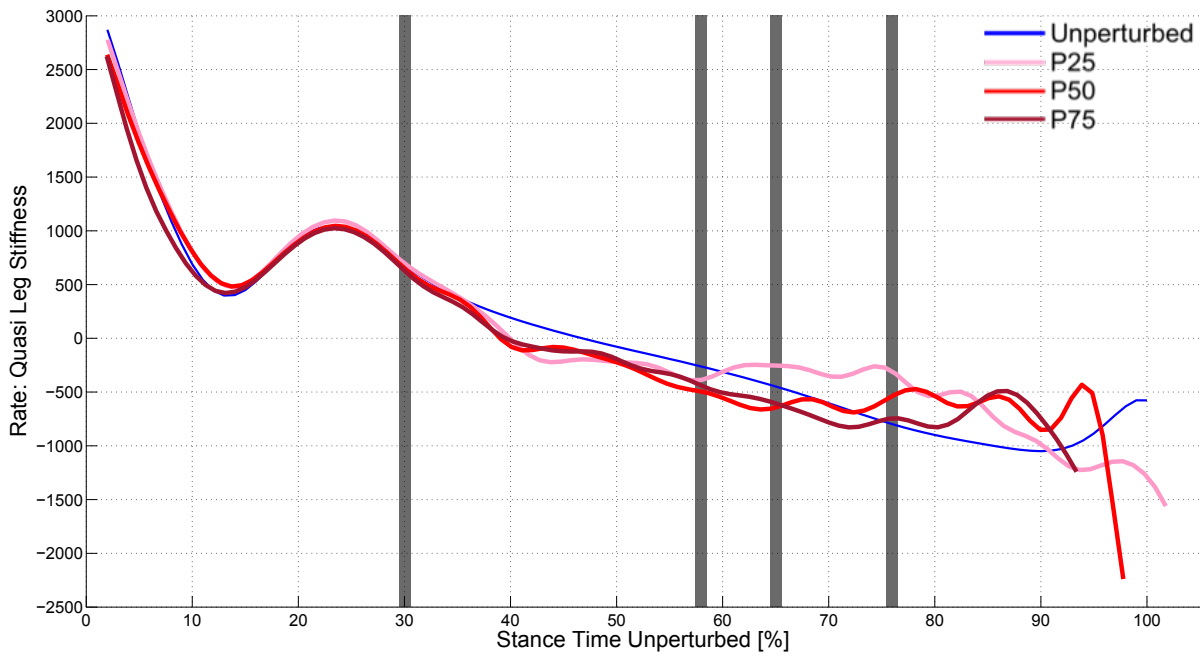


Figure 4.6: *Rate of leg stiffness $\dot{k}Leg$ for unperturbed (blue line) and perturbed (red lines) hops. Different perturbation heights are indicated by different shades of red. Vertical grey bars indicate (from left to right) the instant of perturbation initiation and the instants of acceleration reversal.*

4.3.3. Joint kinematics and kinetics

Joint angles and torques as well as the torque-angle relations of ankle, knee and hip are shown in Figure 4.7 and Figure 4.9. Furthermore, the rate of joint torques is shown in Figure 4.8.

Ankle and knee angles decrease to a minimum (maximum joint flexion) around mid-stance and subsequently increase, whereas the corresponding joint torques show similar but inversed behavior, i.e. they first increase and then decrease. Joint angles do not decrease instantaneously after TD but display a certain delay. This delay increases from ankle to hip; the ankle torque rises progressively in early stance whereas the increase of knee torque only starts at about 10 % of stance time, and hip torque shows a clearly different development over the whole stance. The ankle angle shows the largest angular range compared to knee and hip. Interestingly, the torque range in ankle and knee is almost the same.

Until the perturbation starts (30 % of stance), the joint angle shapes of perturbed (red lines) and unperturbed hopping traces (blue lines) are similar. Afterwards, perturbed traces (red lines) are distinguished from the unperturbed condition with earlier and faster joint extension. After the instant of acceleration reversal (depending on perturbation height), the joint extension slows down, which holds true for all three leg joints. At TO, the leg is more extended compared to unperturbed hopping after perturbations P50 and P75, whereas the leg is less extended after perturbation P25. The peak ankle torques during perturbed hopping do not show a general trend, as the highest peak is displayed by P50 and the lowest peak by P25. This behavior is inverse with respect to knee torques; unperturbed hopping shows the highest peak knee torque of all conditions. In early stance, all ankle torque traces show a similar curvature and progression. After the instant of perturbation initiation, ankle torque traces depend on perturbation height. Compared to unperturbed hopping, torques decrease earlier and faster for P25 (light red line). In contrast, torques of P50 (intermediate red line) and P75 (dark red line) increase to a higher level, but then decrease much faster compared to unperturbed hopping and P25. After the instants of acceleration reversal, the ankle torques of perturbed hopping decrease. The ankle torque rates of perturbed hopping during stance are shown in Figure 4.8 (upper graph). The rates of perturbed hopping suddenly drop at around 37 % of stance, which is in line with the beginning of platform movement. Furthermore, it is shown that the rates increase after the instants of acceleration reversal and even surpass the trace of unperturbed hopping.

Until the instant of perturbation initiation, knee torques of perturbed and unperturbed hopping follow a similar trend: 0 – 10 % no increase, 10 – 30 % increase. Compared to unperturbed hopping, traces of P25 increase earlier and faster whereas traces of P50 and P75 increase slightly later and more slowly, respectively. Afterwards, perturbed hopping traces increase much more slowly, which is in line with a drop in their rates (Figure 4.8, middle graph) in response to the beginning of platform movement (around 37 % of stance). The lower rates also result in lower peak magnitudes and slightly earlier decrease in knee torques. Compared to unperturbed hopping, the knee torques decrease less rapidly after the instants of acceleration reversal, which corresponds to larger increases in torque rates.

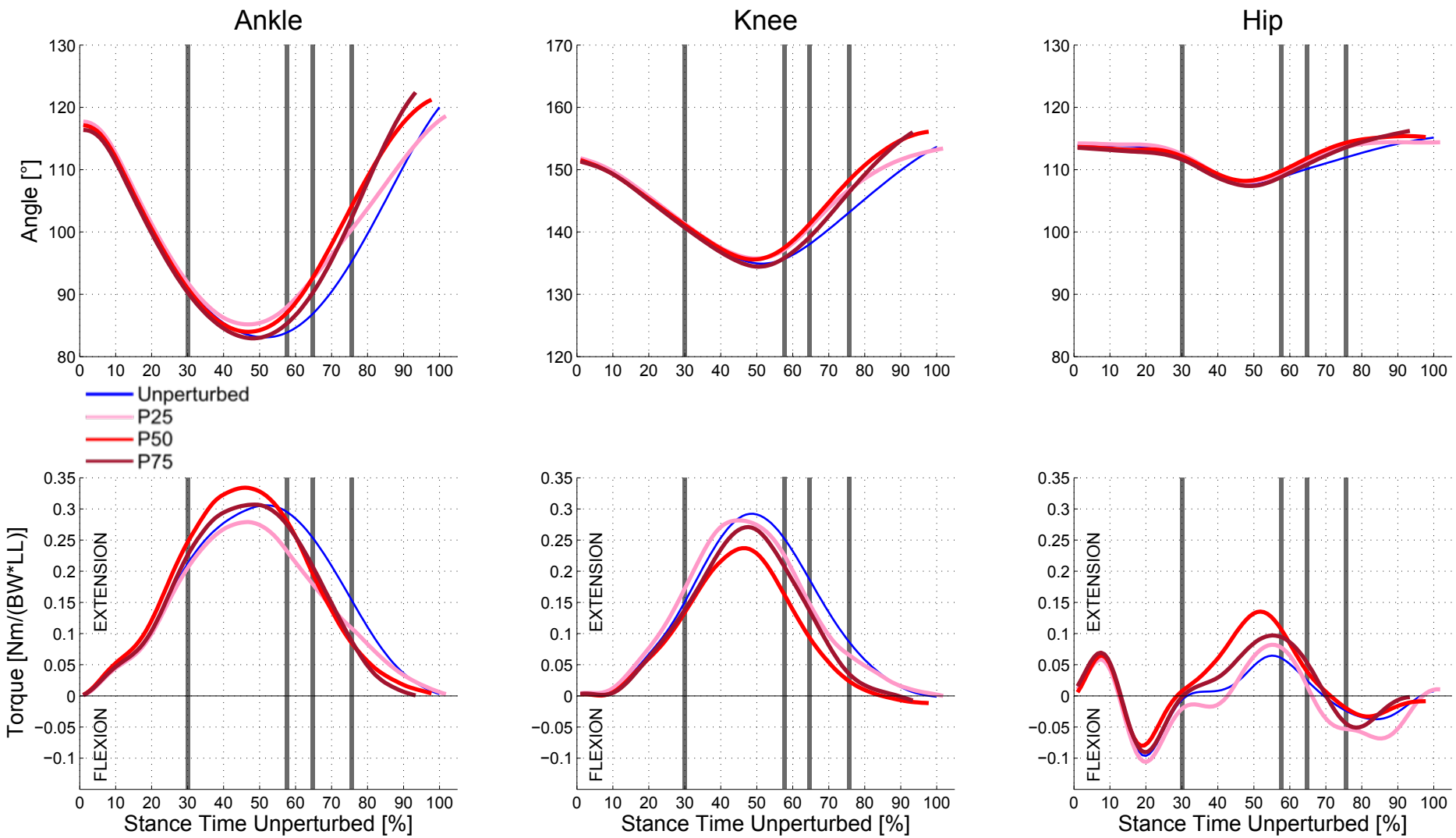


Figure 4.7: *Joint angles (upper graphs) and torques (lower graphs) for unperturbed (blue lines) and perturbed (red lines) hopping. Different perturbations are indicated by different shades of red. Vertical grey bars indicate (from left to right) the instant of perturbation and the instants of acceleration reversal.*

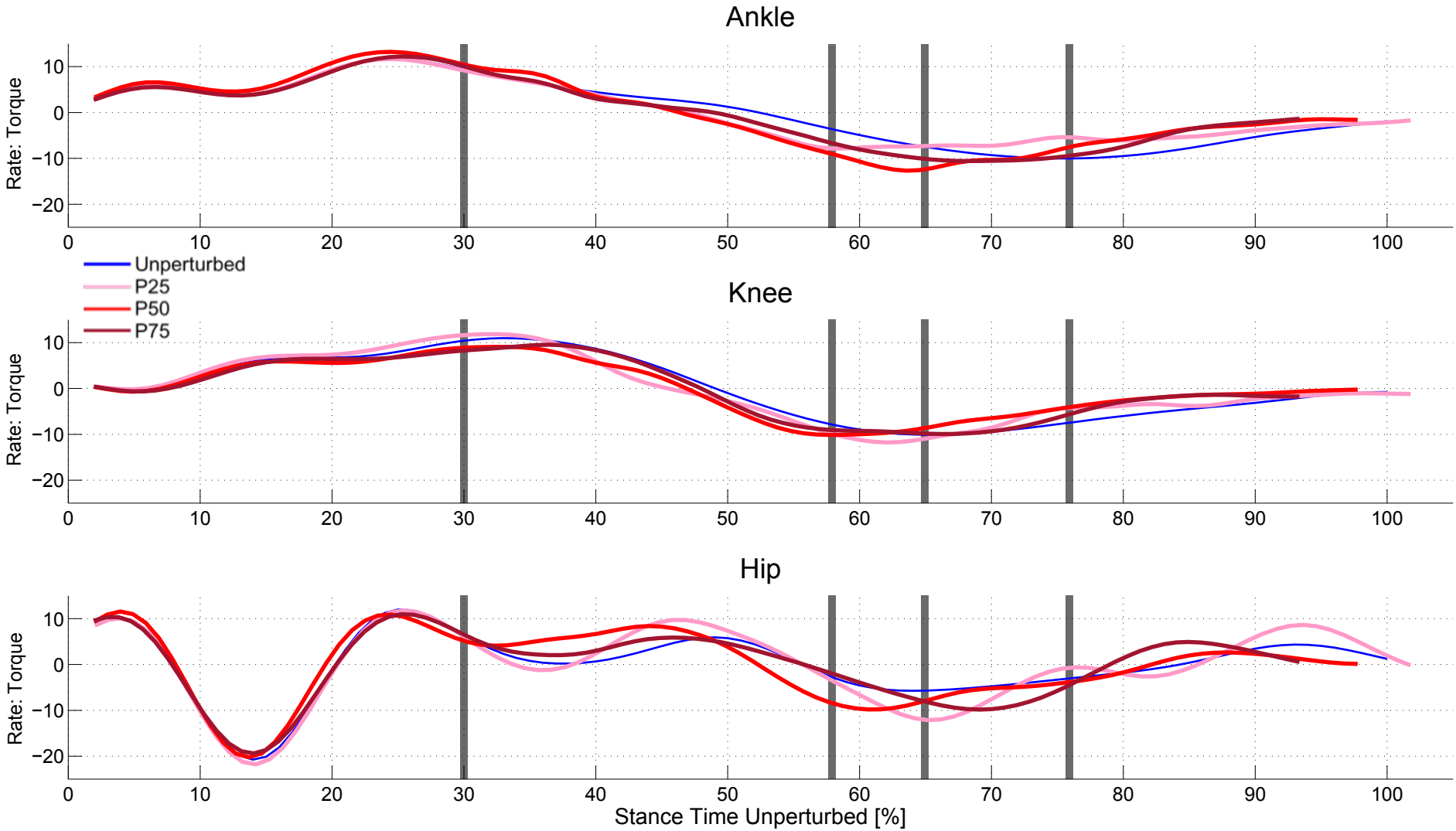


Figure 4.8: *Rates of joint torques for unperturbed (blue lines) and perturbed (red lines) hopping. Different perturbations are indicated by traces in different shades of red. Black diamonds indicate the instant when platform acceleration begins. Black triangles indicate the instant of acceleration reversal.*

During early stance, hip torques (Figure 4.7, lower right-hand graph) show an unsteady development although hip angles do not change much in this phase (Figure 4.7, upper right-hand graph). Hip angles of perturbed and unperturbed hopping remain at a similar constant level. With the instant of perturbation initiation, hip angles of unperturbed hopping decrease until mid-stance and subsequently increase until TO. This is similar to perturbed hopping, whereas the traces increase faster and decrease again slightly in late stance. After perturbation initiation, hip torques of unperturbed hopping remain at a similar level (30 – 45 % of stance phase), then increase rapidly (45 – 55 %), decrease until the beginning of late stance (55 – 85 %) and increase again until TO (85 – 100 %). During this phase, torques of perturbed hopping differ strongly in comparison to each other and also in comparison to unperturbed hopping. In the first part of this phase (30 – 40 %), torques of perturbed hopping are still negative (indicating joint flexion) and decrease slightly, whereas torques of P50 and P75 are already within the positive range. In the following, the torques of perturbed hopping increase faster (40 – 55 %) than unperturbed hopping, after which they also decrease faster (55 – 70 %). In the first half of late stance (70 – 85 %), torques (perturbed as well as unperturbed) further decrease but increase again in the second half (85 % – end) of late stance. During late stance, traces are unsteady and exhibit small oscillations.

From 30 – 50 % of the stance phase onwards, hip torque rates (Figure 4.8, bottom graph) of P50 and P75 decrease less compared to unperturbed hopping, which results in higher torque levels (Figure 4.7), especially in P50, which displays the highest hip peak torque.

In the following period (50 – 80 %), specific differences between P50 and P75 from unperturbed hopping are found. The hip torque rate of P50 suddenly drops. Hence hip torque P50 decreases much faster compared to unperturbed hopping. However, it does not decrease below the level of unperturbed hopping at the end of this period (80 %). In contrast, the hip torque rate of P75 does not differ greatly from unperturbed hopping (50 – 62 %) but decreases for a longer period (until 69 %), which results in a lower torque level compared to unperturbed hopping (79 %). In the last period (80 % – end), both P50 and P75 hip torque rates are higher compared to unperturbed hopping, which results in higher hip torques during this phase.

4.3.4. Joint characteristics

Joint stiffness of unperturbed and perturbed hopping is shown in Figure 4.9. In unperturbed hopping (blue lines), ankle and knee torque-angle relations (TAR) show an almost linear increase and decrease. Knee joint stiffness is clearly higher than ankle joint stiffness.

Ankle TAR (Figure 4.9, red lines in left-hand graphs) of all perturbation heights shows a similar pattern to that of unperturbed hopping until perturbation initiation (indicated by black diamonds). Afterwards all perturbed traces show larger negative work loops until the instant of acceleration reversal (indicated by black triangles). During this phase, the TAR traces of P25 and P75 are shifted downward and upward, respectively, in relation to unperturbed hopping. The trace of P50 shows the largest difference from unperturbed hopping with steeper slopes (rising and falling) and the largest negative work loop compared to the other perturbation heights. Towards TO the perturbed hopping traces converge to the trace of unperturbed hopping, whereby P75 shows the closest fit.

The knee TAR of unperturbed and perturbed hopping (Figure 4.9, center graphs) exhibits an initial plateau (low stiffness), constant slope until maximum angular displacement and torque, and finally a descending limb until TO. The slope (joint stiffness) increases with the amount of joint flexion. Perturbed hopping TAR differs from unperturbed hopping with respect to the slopes and the size of negative work loops. However, the differences decrease with increasing perturbation height.

The hip TAR of unperturbed hopping (Figure 4.9, blue lines in right-hand graphs) shows non-linear development with rapid (positive and negative) torque excursions at the beginning, followed by a plateau phase, which transitions into a positive work loop until the peak of angular displacement and torque. Afterwards unperturbed hip TAR decreases and falls below zero, but increases again until TO; which forms a valley-like shape in the final phase.

Perturbed hip TAR traces (red lines) resemble those of the unperturbed condition until the instant of perturbation initiation (Figure 4.9, black diamonds). In contrast to unperturbed hopping, there are no plateau phases in the perturbed hopping traces, which can be seen by changing angular displacement without any changes of hip torque (Figure 4.9, blue lines in the right-hand graphs). During this period, the trace of P25 decreases slightly and the traces of P50 and P75 immediately increase, whereby P50 increases more rapidly than P75. Compared to unperturbed hopping, work loops of perturbed hip TAR are much larger. Furthermore, the work loops of perturbed hopping hip TAR seem to be larger. In the following, the traces decrease similarly to the unperturbed hopping condition. With the instant of perturbation reversal, the perturbed TAR traces flatten, which also affects their subsequent development during late stance, resulting in smaller valley-like shapes compared to unperturbed hopping. This effect is reduced with increasing perturbation height.

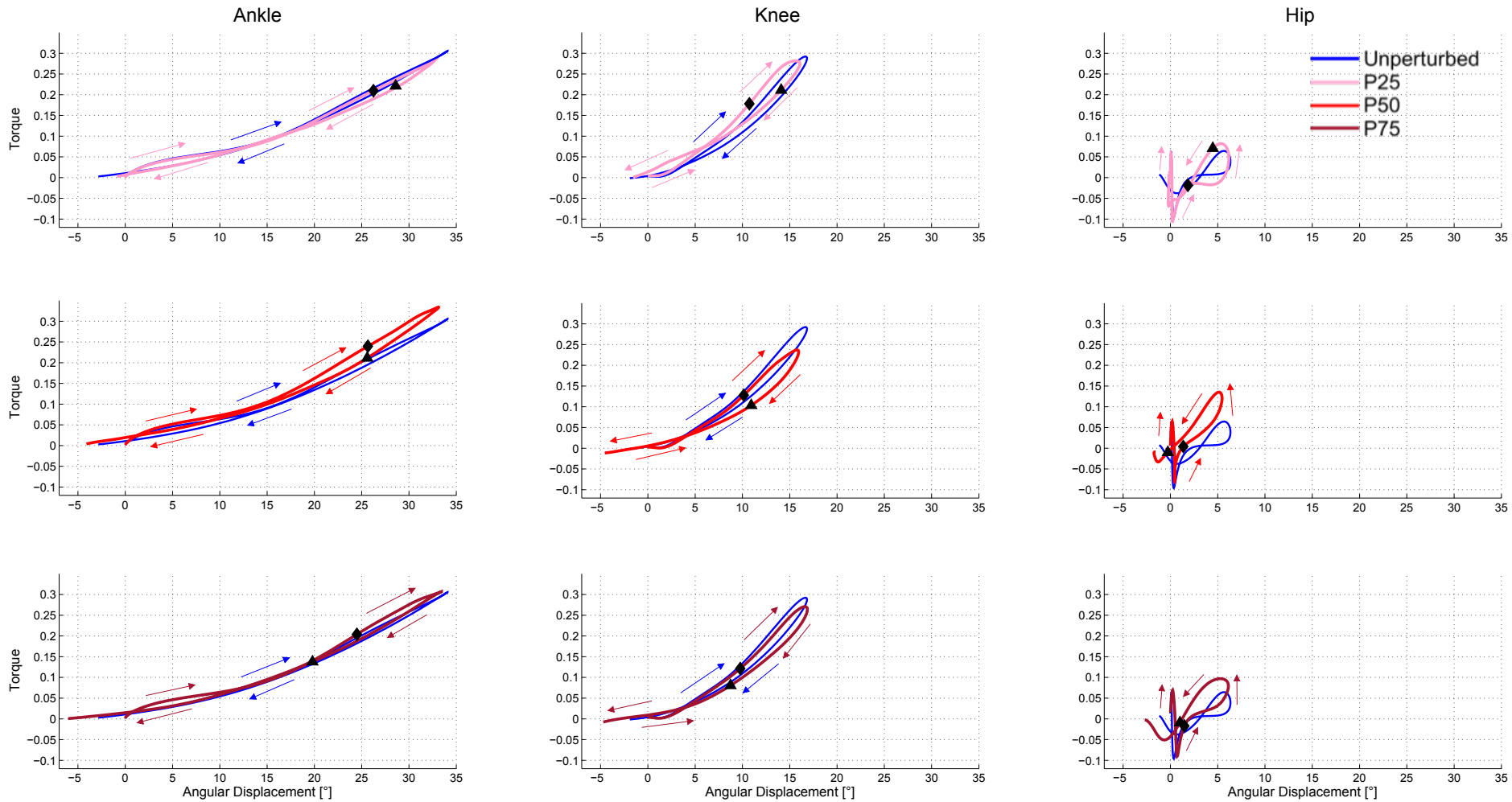


Figure 4.9: *Relation of joint torque to angular displacement of ankle (left graphs) and knee (right graphs) in unperturbed (blue lines) and perturbed (red lines) hopping. Different perturbations are indicated by traces in different shades of red. Black diamonds indicate the beginning of platform acceleration. Black triangles indicate the instant of acceleration reversal.*

4.3.5. Statistical comparison

We investigated whether subjects showed similar hopping behavior during unperturbed hopping compared to unperturbed hopping. Therefore, we conducted repeated measures ANOVA ($p < 0.05$) for dependent samples to verify whether differences in several variables (Table 4.3) for a series of consecutive unperturbed hops (4 hops before the perturbation) are non-significant. Results show no significant differences for any tested variable, indicating that all subjects show similar hopping behavior during unperturbed hopping.

Table 4.3: *Results from ANOVA, comparing the grand mean over all subjects for unperturbed hops.*

Variable	P25		P50		P75	
	F-statistic	*p-value*	*F-statistic*	*p-value*	*F-statistic*	*p-value*
Stance time	0.0046	0.9996	0.0194	0.9962	0.0099	0.9986
F_{max}	0.0004	1.0000	0.0228	0.9952	0.0082	0.9990
ΔLL_{max}	0.8723	0.4656	0.1404	0.9350	0.3314	0.8027
k_{max}	0.0483	0.9857	0.0225	0.9953	0.0429	0.9880
k_{rising}	0.0344	0.9913	0.0183	0.9966	0.0403	0.9890
$k_{falling}$	0.0071	0.9992	0.0060	0.9993	0.0066	0.9993

For the statistical comparison of unperturbed and perturbed hopping, we performed t-tests for independent samples to verify whether differences between unperturbed and perturbed hops are significant. Results (Table 4.4) show only a few significant differences: stance time (P75), $k_{falling}$ (P25), CEL (P50 and P75), ankle angle A-Angle (P25 and P50), ankle torque A-Torque (P75) and knee torque K-Torque (P50).

Table 4.4: *Hypothesis test result (h) and level of significance (p-value) from t-test comparing different variables of unperturbed and perturbed hopping with respect to the different perturbation conditions.*

Variable	P25		P50		P75	
	h	*p-value*	*h*	*p-value*	*h*	*p-value*
Stance time	0	0.1582	0	0.0812	1	0.0000
F_{max}	0	0.6897	0	0.4852	0	0.4228
ΔLL_{max}	0	0.2531	0	0.5745	0	0.6909
k_{max}	0	0.1891	0	0.4646	0	0.6535
k_{rising}	0	0.2000	0	0.4854	0	0.6934
$k_{falling}$	1	0.0359	0	0.9325	0	0.7746
CEL	0	0.0533	1	0.0021	1	0.0073
A-Angle	1	0.0225	1	0.0085	0	0.1372
K-Angle	0	0.0854	0	0.2546	0	0.9753
H-Angle	0	0.6549	0	0.5617	0	0.3376
A-Torque	0	0.9244	0	0.5735	1	0.0386
K-Torque	0	0.0884	1	0.0234	0	0.3052
H-Torque	0	0.9726	0	0.3673	0	0.0502

4.4. Discussion

In this study, we investigate the biomechanical response of the human body to sudden ground level perturbations in human hopping on the spot. Based on the muscle-tendon dynamics of the leg extensor muscles, we expected the human body to respond to a lowering in ground level by a drop in leg force and leg stiffness. The analyses on sudden ground level drops in stance revealed that the human neuro-mechanical system is quite robust with respect to sudden ground level perturbations and that the motor control response is in relation to changes in surface acceleration. The results indicate robust leg function even in the case of large ground level drops (up to 75 mm), demonstrating the ability of the human neuro-muscular system to cope with unexpected perturbations (e.g. yielding ground) during hopping on the spot. This is in line with previous studies on running (Ferris et al., 1999, 1998; Kerdok et al., 2002) and hopping (Farley et al., 1998; Ferris & Farley, 1997; Moritz & Farley, 2004) on compliant ground. The reduced leg compression (due to the lowering of the ground) leads first to a slightly reduced leg stiffness rate, which was then compensated by a greater stiffness rate in the late stance phase. The development of the dynamic leg stiffness thus follows the general trend of the acceleration profile of the perturbation platform: downward acceleration causes a drop in the stiffness rate, positive acceleration causes a rise in the stiffness rate. The acceleration of the perturbation platform also leads to a shift in the leg force. Assuming a force feedback for the leg extensor muscle control (Geyer et al., 2003), this would result in changed extensor muscle activity and hence could modulate muscle (and leg) stiffness. Such a relationship was not investigated here and remains for further studies.

4.4.1. Leg behavior

Vertical GRF (Fz) of unperturbed hops exhibits a bell shape as found in other experimental studies on human hopping (Ferris & Farley, 1997; Moritz & Farley, 2005; Pezeshk, Sadeghi, Safaeepour & Zadeh, 2017; Riese et al., 2013; van der Krogt et al., 2009) indicating that hopping was only disturbed by the active lowering of the platform. In contrast, Fz of the perturbed hops shows clear differences from the unperturbed condition (see Section 4.3.1). Similar to other studies on hopping (Moritz & Farley, 2005; Pezeshk et al., 2017; van der Krogt et al., 2009), the Fz of unperturbed and perturbed hopping shows an increasing slope during early stance (Figure 4.2, 0 – 30 %).

Effective leg stiffness k_{max} (Table 4.2) during unperturbed and perturbed hopping is higher compared to other studies (Farley et al., 1998; Farley & Morgenroth, 1999; Moritz & Farley, 2004). This is surprising, especially in the unperturbed condition, as the perturbation platform is rather stiff (surface oscillations around 0.02 mm). In this context, previous studies on human hopping and running (Farley et al., 1998; Ferris & Farley, 1997; Ferris et al., 1999, 1998; Kerdok et al., 2002; Moritz & Farley, 2004; van der Krogt et al., 2009) show that leg stiffness is modulated with surface stiffness to realize stable hopping: high surface stiffness requires low leg stiffness, whereas low surface stiffness requires high leg stiffness. The experimental design of the present study did not include trials that did not introduce any perturbations. However, since subjects knew that perturbation would be introduced, they may have stiffened their legs during hopping in order to minimize stance time. This precaution might serve as a strategy to avoid large disturbances of the stable hopping pattern due to the ground level perturbation.

Thus, subjects may use this strategy to cope with the expected surface change and to be prepared for any perturbation following touchdown.

In contrast to the results of other studies (Kuitunen, Ogiso & Komi, 2011; Moritz & Farley, 2004, 2005), the observed joint angles and torques show delays (i.e. retarded decrease) during early stance in both hopping conditions (Figure 4.7, unperturbed and perturbed hopping). The delayed development is rather small (~0 – 3 % of stance) for ankle and knee joint angle development but becomes more extended in the hip (~0 – 25 % of stance). In the joint torques, delayed development is found in the knee (0 – 10 % of stance). From the joint angle development, the knee-hip system first acts in a similar way (potentially synchronized) after touchdown and subsequently deviates. The ankle flexes first and is then followed by the knee-hip system. The COM is lowered without any change of trunk inclination. We found that knee torques merely increase after 10 % of unperturbed stance time, whereas ankle torques decrease slightly after 10 % of unperturbed stance time. This indicates a joint-dependent response to the ground level perturbation and questions the specific role of the foot in detecting the change in the environment. Models similar to the VPP concept for the hip function in locomotion (Maus et al., 2010) could be used as a template to investigate the neuro-muscular response to ground change in future gait models.

Although the general behavior of joint angle and torque during unperturbed hopping was similar to recent experimental studies (Farley & Morgenroth, 1999; Kuitunen et al., 2011; Moritz & Farley, 2005), the observed adaptations of joint stiffness in response to the different perturbation conditions (P25 to P75) are not consistent. The different curves in Figure 4.9 indicate that knee joint stiffness changes in response to P25, ankle and hip joint stiffness in response to P50 and only hip joint in response to P50. Besides additional adaptation of hip joint stiffness in response to P50, no further significant adaptation of joint stiffness is observed. Although, there is generally only one joint that responds most to the perturbations, while the other joints exhibit similar joint stiffness, no clear pattern of balance mechanisms is found. However, ankle joint torque-angle curves are very similar to the experimentally observed force-length (FL) curves of the leg but clearly differ in the P50 condition from the unperturbed hopping condition. This contrasts with the results of Farley and Morgenroth (1999), who found that the primary mechanism for leg stiffness adjustment is the adjustment of ankle stiffness.

Interestingly, the rate of dynamic leg stiffness ($\dot{k}Leg$) seems to be a feasible and useful tool to explain changes of leg stiffness during highly dynamic movement tasks such as hopping. With respect to the introduced vertical ground level perturbation and its acceleration profiles (implemented in the perturbation profile to change ground level height), changes in $\dot{k}Leg$ are related to changes in ground acceleration (at least with a very small delay). Hence, the progression of $\dot{k}Leg$ (Figure 4.6) shows distinct changes at the instants when the downward ground level movement is initiated and when the perturbation platform begins to reduce the downward movement (i.e. when the numerical value of the platform becomes positive).

The rapid lowering of the surface may reduce the leg shortening (due to the compression of the leg during stance in hopping) and thus decrease the lengthening rate of the extensor muscles. By implication, a rapid rise of the surface may result in increased leg shortening and thus an increasing shortening rate of the extensor muscles. With respect to muscle-tendon dynamics, this might explain the reduced leg force (Figure 4.2) and leg stiffness (Figure 4.5) during

perturbed hopping observed in this study. Observed changes of *kLeg* and $\dot{k}Leg$ (Figure 4.5 and Figure 4.6) in response to changes of the ground level acceleration contribute to the validity of these proposals.

4.4.2. Leg robustness

Our findings show that humans can cope with sudden ground level perturbations during the stance phase while hopping. Although the Fz of perturbed hopping (Figure 4.2) shows clear differences from unperturbed hopping, the global leg function does not change greatly (Figure 4.5). Interestingly, the results show that $\dot{k}Leg$ changes with changing surface acceleration (Figure 4.6) and, consequently, also affects *kLeg* (this effect is discussed below). This is in line with previous results showing that runners adjust leg stiffness to surface stiffness within one step (Ferris et al., 1998, 1998), although the question remains open as to which biomechanical mechanism realizes the observed leg stiffness adjustments. FL relations (Figure 4.4) suggest that as a mechanical system the human leg is quite robust with respect to the introduced ground level perturbations. Leg stiffness during the perturbed hops increases slightly compared to the unperturbed condition. To further investigate this finding, we compared different biomechanical aspects with respect to leg stiffness such as k_{max}, k_{rising}, $k_{falling}$ and the CEL. The resulting mean values (Table 4.2) also indicate robust leg behavior. Hence, also these more detailed biomechanical aspects of perturbed hopping do not differ greatly from unperturbed hopping. This is supported by statistical analyses (Table 4.4), which only show significant differences in $k_{falling}$ (in P25) and CEL (P50 and P75). Differences in the other tested variables regarding leg stiffness are non-significant.

The time difference between the instant of perturbation initiation and the observed drop in $\dot{F}z$ and $\dot{k}Leg$ is around 6 % of unperturbed stance time (Figure 4.3 and Figure 4.6), which corresponds to 15.88 ms (Table 4.2). Hence, changes in *kLeg* must be realized by a mechanism other than reflexes or high-level motor control due to the short time period. We expect that the elastic properties of the leg, such as tendons and muscles, contribute to our findings regarding the effects on the muscle dynamics of sudden changes in ground level acceleration during stance (this has been already discussed in the previous section). Previous results (Moritz & Farley, 2004; van der Krogt et al., 2009) show that passive leg and muscle preflex mechanics may compensate for sudden changes in surface stiffness. Van der Krogt et al. (2009) found that in simulated human hopping passive adaptations in leg stiffness are caused by changes in joint angles and corresponding muscle lengths. Furthermore, van Soest and Bobbert (1993) suggest that muscle properties may generate a peripheral feedback mechanism that has no time delay and in simulations they show that this zero-lag peripheral mechanism can cope with a certain range of perturbations. However, introduced perturbations (van Soest & Bobbert, 1993), such as initial leg angle position or angular velocities, make comparisons with the results of the present study more difficult.

Decreasing CEL during perturbed hopping (Table 4.2), which means that the leg becomes softer and behaves in a less spring-like manner, indicates that the elasticity of the leg is reduced and results in less spring-like leg behavior. This might be a consequence of the observed increased leg stiffness (Table 4.2). Considering the increased leg stiffness could imply that the leg behavior is more muscle-driven, i.e. leg compliance caused by elastic structures is actively

modulated by muscle control; as reported, for example, in Loram et al. (2004) on human standing. In this way, control of leg behavior may also rely to a greater extent on active muscle control (e.g. mediated by sensor feedback such as force, velocity or length feedback). In addition, the findings in this study show that leg stiffness and GRF are modulated in relation to surface acceleration, i.e. they drop during negative (downward) acceleration and increase during positive (upward) acceleration. Taken as a whole, this supports the idea that the adjustment of leg behavior in response to vertical ground level perturbations is modulated by sensory feedback, such as positive force feedback, (Geyer et al., 2003). This is in line with the findings of Schumacher and Seyfarth (2017) suggesting a favorable combination of force and length feedback as a sensory motor control mechanism to enable stable hopping in a neuro-muscular model.

Riese et al. (2013) found that variability in the leg-spring parameters (such as leg length and leg stiffness) is an important system property and might not only be caused by external perturbations. It is still not clear how the neuro-musculoskeletal system controls the biomechanical leg parameters. As mentioned above, positive force feedback mechanisms may play an important role in adjusting leg stiffness rates in response to sudden ground level changes. This is in line with the response of the force-modulated compliant hip (FMCH) control as shown in biomechanical and neuromuscular models of postural stability (Sharbafi, Ahmadabadi, Yazdanpanah, Nejad & Seyfarth, 2013). With the help of such extended biomechanical and neuromuscular models, the influence of ground level perturbations on gait stability and balance control can be further investigated. In addition, the changing rates of GRF and *kLeg* can be used as tools to assess the modulation of leg stiffness and leg force, respectively, and thus help to interpret leg behavior in response to unexpected perturbations. In this way, it is also possible to investigate oscillations in Fz and *kLeg* after the instant of acceleration inversion (Figure 4.2 and Figure 4.5).

5. Conclusions and Outlook

5.1. Conclusions

In this thesis, we explored how humans respond to external perturbations and examined which coping mechanisms (e.g. changed kinematics) and strategies (e.g. foot placement strategies, feedback control) are applied to maintain postural balance in order to prevent falling. To this end, leg behavior focusing on muscular-mechanical properties and mechanisms was investigated with respect to the locomotion sub-functions (Sharbafi & Seyfarth, 2017); i.e. standing (axial leg function), leg swinging (rotational leg function) as well as balancing and posture balance control (Seyfarth et al., 2012).

In a review, we systematically collected previous research results thus providing insights into how leg function responds to external perturbations and selected motion tasks. Based on the research overview, follow-up experiments were designed addressing the ability of humans to cope with external perturbations with respect to axial and rotational leg function. The latter aimed at evaluating the role of mono- and biarticular muscles in the alignment of the ground reaction force (rotational leg forces) in response to horizontally introduced external forces. Regarding the axial leg function, the ability to adapt leg stiffness in order to maintain steady movements in response to vertical ground level perturbations was investigated. In the following, we will first briefly summarize and discuss the main insights obtained from our research and then discuss the impact of this work for future research and possible applications from different perspectives.

The perturbation matrix (PMA)

A systematic literature review was undertaken (Chapter 2) analyzing biomechanical aspects in response to external perturbations during selected motion tasks. The PMA maps experimental studies as well as simulations and models of human behavior. In this analysis, predominantly experimental work is represented, which illustrates the research focus in these studies. The improved understanding of human balance mechanisms and coping strategies not only serves as an inspiration for the design and control of assistive devices but also highlights possibilities for future research. The PMA offers a tool for identifying gaps in research targeting the identification of human movement strategies and conceptual models. Consequently, future studies should not only focus on measuring or simulating singular responses, but should rather consider conceptual models in an overarching context. On the one hand, studies could be based on conceptual models such as the virtual pivot point (VPP) and force modulated compliant hip (FMCH) model (Sharbafi, Ahmadabadi, et al., 2013; Sharbafi, Maufroy, et al., 2013), i.e. to measure human and behavioral characteristics allowing conclusions to be drawn with respect to these models. On the other hand, studies could be designed to investigate the validity of these models in different contexts. This could be either to verify the concept in humans with challenging environmental influences (e.g. external perturbations) or to test the concept with humans *in-the-loop*, e.g. with assistive devices such as exoskeletons. In this context, experiments with the LOPES II exoskeleton have already shown that motor control concepts based on the VPP and FMCH model can support humans in walking and also increase walking efficiency (Zhao, Sharbafi, Vlutters, van Asseldonk & Seyfarth, 2017). In accordance with the test trilogy

(Kalveram & Seyfarth, 2009), it is not only important to verify results from experimental and simulated work by reciprocal confirmation of coherences but also by transferring insights to robotic devices thus verifying their general validity in a conceptual but real-world system.

Responses to different perturbations

Specified areas of research were reviewed (Chapter 2) to identify balance mechanisms and strategies used to prevent imbalance and falls. The findings represent a summary of original research articles on already investigated human balance strategies and mechanisms with respect to specified motion tasks and perturbation characteristics. Through the review, we learned that humans adjust their movements (by applying a certain strategy) not only to the environmental context (e.g. when walking on even ground vs. slopes or climbing stairs) but also in accordance to the state of their motion (i.e. current phase of gait, center of mass (COM) position) and in relation to the type of perturbation (e.g. changes in ground or external forces).

Considering conceptual models for posture control (e.g. the virtual pendulum concept) helped us to evaluate the findings in a broader context. This also allowed us to find supplementary coherences such as the role of biarticular leg muscles for trunk stabilization as well as swing leg placement in response to external perturbations. Such structural elements and motion strategies enable humans to employ versatile motor control strategies that are not only perturbation-specific but can also be applied in response to similar perturbations and during different motion tasks.

Rotational leg function

A conceptual model (Rode & Seyfarth, 2013) suggests that appropriate segment length (1:1 thigh to shank length ratio) and moment arm ratios of two-joint muscles (2:1 for hip vs. knee, and for ankle vs. knee) may help to decouple postural control (via biarticular muscles) from axial leg force production (via monoarticular muscles). To validate the model, the role of mono- and biarticular muscles in the alignment of non-axial leg forces was studied (Chapter 3). Therefore, quasi-static horizontal forces were introduced during upright human stance and changes in corresponding leg muscle activity were measured. The results showed that biarticular muscles strongly contribute to the redirection of the ground reaction forces (GRF) in order to maintain an upright posture. Furthermore, advanced statistical analyses of muscle activity patterns revealed linear force effects, effects of different initial leg configurations, and a combination of the two thus indicating the capacity and general applicability of this concept.

Co-activation of antagonistic muscles

Conceptual models can help to observe and support specified behavior such as different locomotion patterns (walking and running) and allow motor responses to certain perturbations to be predicted. However, most models are quite simple and describe only a finite complexity of the human motor (control) system. Moreover, they are not appropriately designed for balancing. Thus, for a better understanding, the experimental work (Chapter 3) on perturbed standing validated the hypothesis that muscles are not designed for single purposes.

We found that (antagonistic) mono- and biarticular muscles were co-activated in response to different experimental conditions. This indicates that distinct connections in the neural system might compensate for limited muscle capacity or functionality. Results from this work suggest that monoarticular muscles also contribute to joint stability when capacities of biarticular muscles are exceeded.

Furthermore, it is known that biarticular muscles align GRF and also provide axial energy transfer, e.g. for ankle push off (Jacobs et al., 1993; van Leeuwen & Spoor, 1992). In this way, co-activation of antagonistic (mono- and biarticular) muscles may serve to fine-tune the necessary energy transfer to realize the joint function required in order to maintain an upright posture; and additionally, preserve the ability to align horizontal GRF (non-axial leg function) to maintain balance and prevent falling.

Insights into the complex human motor control system, such as the versatile function of biarticular muscles, may lead to a better synthesis of humans and machines and thus enable more effective control and support. Hence, implementing biarticular structures in robots led to simple and efficient control mechanisms for GRF direction control in the BioBiped3 robot (Sharbafi et al., 2016).

Axial leg function

In the second experimental study (Chapter 4), the response of the human body to sudden ground level perturbation in human hopping on the spot was investigated. Based on the muscle-tendon dynamics of the leg extensor muscles, it is expected that the response of the human body to a lowering in ground level results in a drop in leg force and leg stiffness. The results indicated robust leg function, demonstrating the ability of the human neuro-muscular system to cope with unexpected perturbation (e.g. yielding ground) while hopping. However, the overall capacities of the robustness of the leg have not yet been completely quantified. Further research is needed to identify which elastic structures (e.g. tendons, ligaments, etc.) contribute to leg robustness, where the limits are and what role is played by active motor control. Therefore, we suggest that a study similar to this experimental study should be conducted, introducing unforeseen changes of ground level during an ongoing motion task (here: hopping). Nevertheless, perturbation characteristics should include variations in speed and acceleration rather than perturbation height.

Modulation of leg stiffness

The analyses of the second study (Chapter 4) revealed that the human leg (seen as a neuro-mechanical system) is quite robust with respect to sudden ground level perturbations. Results indicate that muscle responses and motor control are sensitive to changes in surface acceleration. The amounts of adjustments made were related to the different perturbation characteristics and remained constant throughout this perturbation (i.e. lowering of the ground). The earlier reduced leg stiffness was compensated in relation to ground acceleration (i.e. the instant of ground level acceleration inversion). This indicates that the mechanical response may be modulated by muscle length and force feedback.

Tools for response investigation

In the study on perturbed hopping (Chapter 4), dynamic leg stiffness (i.e. leg stiffness for each instant of the stance phase) was calculated. The rates of GRF and dynamic leg stiffness revealed the adaptations of leg function in response to sudden ground level perturbations and thus provided insights into balance mechanisms. In this way, derivatives of leg stiffness and GRF might be considered as tools for the advanced investigation and evaluation of human leg function. This allows us to quantitatively assess leg function in various contexts such as environmental influences and external perturbations. The understanding of the robust human (motor) control system can thus be further improved.

External perturbations were used to systematically modify task execution in standing and hopping; which might be considered variations of motion patterns. This variation is a prerequisite for the assessment of sensor-motoric loops and control mechanisms. In this context, assistive devices may not only serve to train patients and demonstrate the validity of current motor control concepts. They may also be used to introduce systematic variations to further improve the understanding of the motor control system by active support or constraint of the human leg function during task execution. Thus, applying perturbations with different characteristics (e.g. various accelerations, direction) as a tool in research may reveal specific conditioning of the leg function providing new insights into human motor responses. Additional research remains to be conducted to further validate the relationship between perturbation characteristics and motor response.

5.2. Outlook

This thesis identified the ability of the human sensory system to perceive changes in ground level acceleration as a key factor for (quasi-reflexive) muscle responses leading to robust hopping patterns. These insights may be taken into account in the design of future experimental work introducing perturbations to subjects while executing (loco-)motion tasks. Observed human robustness (of the locomotor system) in response to large external perturbations during cyclic motion tasks could be taken as an indicator of a change of paradigm in designing studies. This would mean considering asymmetric motion patterns for the validation of the human neuro-muscular system, rather than large mechanical disturbances (which may cause injury). The results from the literature review helped us to obtain a better overview of how humans (typically) respond to certain external perturbations. Identified *humanlike* response patterns could serve as a reference in the rehabilitation of affected humans (e.g. after stroke or if suffering from diseases) or for the control of exoskeletons/humanoid robots. The contribution of biarticular leg muscles to posture control in stance can serve as an inspiration for the design of future humanoid/bipedal robots/devices as well as more complex biomechanical models.

The CYBATHLON 2017 (ETH Zürich, 2017) showed that good athletes with passive prostheses still outperform weaker athletes with active (powered) prostheses. The observation remains, however, that if long data processing times and complex engine control are ignored, human beings must usually adapt to the system and not vice versa. Based on this, technical systems should be designed in such a way that a seamless motion adaptation or intention recognition of the user is possible. This is the case with passive prostheses that are adapted to the human body. Furthermore, human balance strategies and mechanisms have not yet been considered in

the design and implementation of technical systems. After all, humans have learned to keep their balance even in highly complex and challenging situations (e.g. parkour, slacklining).

Nevertheless, the question remains of what steps could be taken in order to make technical devices more sustainable so that people in need obtain significant benefits, e.g. being able to carry on their everyday life on their own. To this end, considering current trends in information technology, such as artificial intelligence (AI) and deep learning/big data, might be of help. Today, our society is experiencing a digital transformation, which means that everything is becoming *smart*, i.e. technical devices collect data and use learning algorithms and AI to assist us in our daily life. Manufacturers have already designed very good assistive devices that make everyday life easier. The next steps in this development could be to make the devices even smarter and more user-centered. Smarter means that the devices could be designed to be more customizable such as i-limb quantum hand prostheses where the user can select from 36 grips (pre-programmed or customized) and provide control via gesture, app, muscle control or proximity (Touch Bionics Inc., n.d.). Furthermore, AI that recognizes the environmental context might help to adjust motor control patterns (e.g. crowded places, sports, environment, etc.). This includes the requirement that devices must be user-centered, i.e. that the devices must adapt to the user and not vice versa.

Basic research currently offers promising approaches for this as it directly delivers quasi-user-centered insights. Similar to the benchmarking scheme from Torricelli et al. (2015), the three main chapters (Chapter 2 – 4) of this thesis can be regarded as a framework suggesting consecutive options for the comparative assessment of the human neuro-muscular (motor) control system: the literature review reveals research opportunities and the complementary experimental work shows in an exemplary way how to gather empirical findings. This thesis contributes to improving the current understanding of the human neuro-muscular system.

However, several questions remain open for future research:

- What is the contribution of cognitive perception and movement experience? What is their impact on the robustness of the human neuro-muscular and locomotor system?
- From a more psychological point of view: Do subjects show learning effects (adaptation to the perturbation) and is human motion execution influenced by laboratory conditions?[6]
- Can insights be transferred to real (complex) movements in daily life? Which technologies could support humans in performing effective responses to external perturbations; during daily life as well as in executing high-level motion tasks?

[6] Two bachelor's theses investigating these topics have been completed at the Institute of Sports Science at TU Darmstadt.

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Annex

1) Source code: R-Studio
2) Output from the statistical analyses
    - Experimental condition: AA
    - Experimental condition: AP
    - Experimental condition: SA
    - Experimental condition: SP
    - Experimental condition: VD

Annex 1: Source code: R-Studio

```
library(R.matlab)
### muscle names and experiment names
names <- c("L_BF","L_TA","L_SL","L_ST","L_RF","L_VM","L_VL","L_GT","L_GM", "L_GL",
"R_BF","R_VM","R_GT","R_RF")
experiment <- c("NA_", "AA_", "AP_")

for (ii in 1:length(experiment))
{
  ### load experiment data; NA neck anterior, AA ankle anterior, AP ankle posterior
  data = readMat(paste("EMG_diff_", substr(experiment[ii],1,2),".mat", sep=""))

  for (jj in 1:length(names))
  {

    # data = readMat("EMG_diff_AA.mat")   # ankle anterior
    # data = readMat("EMG_diff_AP.mat")   # ankle posterior
    # data = readMat("EMG_diff_NA.mat")   # neck anterior

    # select muscle, 1-14;  BF  TA  SL  ST  RF  VM  VL  GT  GM  GL  |  BF  VM   GT   RF
    diff <- data$EMG.diff[,jj]
    plot(diff)
    # hypotheses for muscles:
    #                 BF  TA  SL  ST  RF  VM  VL  GT  GM  GL  |  BF   VM   GT   RF
    #hypothesis_NA = [1   0   1   1  -1  -1  -1   1   1   1      1   -1    1    -1]
    # einbeinig: im rechten Bein vor Belastung kein EMG, daher auch keine Synergie;
    #hypothesis_AA = [-1   0   0  -1   1   1   1  -1   0   0     1    0    1    0]
    #hypothesis_AP = [ 1   0   0   1  -1  -1  -1   1   0   0     0    1    0    1]

    # create headers and entries for data, length 54
    proband <- paste("id", rep(1:9, each=6), sep="")
    wdhlg <- rep(1:6,9)
    force <- rep(c(10,10,20,20,30,30), 9)

    # create headers and entries for data, length  162
    kniewinkel <- rep(c(140,155,180), each=54)

    # construct data array of length 162
    my.data <- data.frame(proband,wdhlg,force)
    my.data <- rbind(my.data,my.data,my.data)
    my.data$kniewinkel <- kniewinkel
    my.data$diff <- diff

    ### mit package lme4
    # require(lme4)

    ### fit linear model
    # my.lme0 <- lmer(diff~-1+(1|proband), data=my.data)
    # my.lme1 <- lmer(diff~1+(1|proband), data=my.data)
    # my.lme2 <- lmer(diff~1+force+(1|proband), data=my.data)
    # my.lme3 <- lmer(diff~1+force+as.factor(kniewinkel)+(1|proband), data=my.data)
    # my.lme4 <- lmer(diff~1+as.factor(kniewinkel)+(1|proband), data=my.data)

    ### mit package nlme)
    require(nlme)

    ### Annahme homogener Varianzen; method = ML muss extra angegeben werden
    # my.nlme0 <- lme(diff~-1, random=~1|proband, data=my.data, na.action=na.exclude,
method="ML")
    # my.nlme1 <- lme(diff~1,  random=~1|proband, data=my.data, na.action=na.exclude,
method="ML")

    ### Annahme inhomogener Varianzen; method = ML muss extra angegeben werden
    my.nlme0.var <- lme(diff~-1, random=~1|proband,
weights=varIdent(form=~1|proband),data=my.data, na.action=na.exclude, method="ML")
```

```
    my.nlme1.var <- lme(diff~1,  random=~1|proband, weights=varIdent(form=~1|proband),
data=my.data, na.action=na.exclude, method="ML")
    #my.nlme2.var <- lme(diff~1 + force,  random=~1|proband,
weights=varIdent(form=~1|proband),data=my.data, na.action=na.exclude, method="ML")
    #my.nlme3.var <- lme(diff~1 + force + as.factor(kniewinkel),  random=~1|proband,
weights=varIdent(form=~1|proband), data=my.data, na.action=na.exclude, method="ML")
    #my.nlme4.var <- lme(diff~1 + force + as.factor(kniewinkel) +
force*as.factor(kniewinkel),  random=~1|proband, weights=varIdent(form=~1|proband),
data=my.data, na.action=na.exclude, method="ML")

    ### Ergebnisse in Datei schreiben

    ### komplette Muskelspezifische Ergebnisse
    #sink(paste(experiment[ii],names[jj], ".out", sep=""))
    ### Ergebnisse in Datei schreiben abschalten
    #sink()

    ### Teilergebnisse; alle Muskeln in eine Datei
    sink(paste(substr(experiment[ii],1,2),".out", sep=""), append = TRUE)
    print(names[jj]) # print muscle name
    ### ?bersicht der Ergebnisse des model fit
    # summary(my.nlme0.var)
    #print(summary(my.nlme1.var))
    print(fixef(my.nlme1.var)) # print only fixed effect

    ### ?bersicht der Ergebnisse des model fit
    # summary(my.nlme0.var)
    #print(summary(my.nlme1.var))
    #summary(my.nlme2.var)
    #summary(my.nlme3.var)
    #summary(my.nlme4.var)

    ### Vergleich mit likelihood ratio test
    ### Passiert etwas? --> steigend: intercept > 0, fallend: intercept < 0,
gleichbleibend: p > 0.05
    #print(anova(my.nlme0.var,my.nlme1.var))
    print(pvalue <- anova(my.nlme0.var,my.nlme1.var)$"p-value"[2]) # print p-value for
storage
    ### Hat die Kraft einen Einfluss?
    #anova(my.nlme1.var,my.nlme2.var)

    ### Hat der Kniewinkel einen Einfluss?
    #anova(my.nlme2.var,my.nlme3.var)


    ### Ergebnisse in Datei schreiben abschalten
    sink()
  } #end #jj
} # end #ii

# fixef(my.nlme4.var)
```

Annex 2: Output from the statistical analyses (R-Studio)

- Experimental condition: AA
- Experimental condition: AP
- Experimental condition: SA
- Experimental condition: SP
- Experimental condition: VD

Conf	Model	MUSCLE / VARIABLE	LGT	LRF	LGL	LGM	LSL	LTA	LVM
AA	*Model 1*	Intercept	0,0001380697	0,0367126200	-0,0015740160	0,0109579400	0,0076938920		0,0016251660
		Likelihood-ratio	0,0556949600	17,7270300000	0,6121071000	5,9383690000	4,9905420000		0,4850890000
		p-value	0,8134000000	<.0001	0,4340000000	0,0148000000	0,0255000000		0,4861000000
	Model 2	Intercept	-0,0003743976	0,0126878350	-0,0016179060	0,0086842687	0,0062616280		-0,0106973394
		Force	0,0000261361	0,0012253370	0,0000021659	0,0001183511	0,0000720409		0,0006128426
		Likelihood-ratio	1,4883990000	39,5079900000	0,0005398474	0,5325911000	0,5988885000		6,6436880000
		p-value	0,2225000000	<.0001	0,9815000000	0,4655000000	0,4390000000		0,0100000000
	Model 3	Intercept	0,0002439791	0,0382726394	-0,0006998746	0,0082934330	0,0075937840		-0,0066736760
		as.factor (Kniewinkel)155	-0,0001460375	-0,0002253038	0,0015704852	0,0066390170	0,0000194659		0,0031782970
		as.factor (Kniewinkel)180	-0,0001790826	-0,0047518816	-0,0045328582	0,0019788020	0,0002708072		0,0235160020
		Likelihood-ratio	0,2012431000	1,8557540000	9,1855310000	5,5204450000	0,0198037300		36,3095400000
		p-value	0,9043000000	0,3954000000	0,0101000000	0,0633000000	0,9901000000		<.0001
	Model 4	Intercept	-0,0002833618	0,0151449250	-0,0007401303	0,0065504934	0,0062233050		-0,0190606786
		Force	0,0000258756	0,0011888810	0,0000020354	0,0000894819	0,0000717970		0,0006333703
		as.factor (Kniewinkel)155	-0,0001508311	-0,0020835030	0,0015694410	0,0066733347	-0,0000248394		0,0027110994
		as.factor (Kniewinkel)180	-0,0001144186	-0,0032854990	-0,0045350460	0,0020221948	0,0001473748		0,0234714321
		Likelihood-ratio	0,1489597000	0,8068837000	9,1855200000	5,3426630000	0,0081574480		37,9043600000
		p-value	0,9282000000	0,6680000000	0,0101000000	0,0692000000	0,9959000000		<.0001
	Model 5	Intercept	0,0003300597	0,0080963782	-0,0001597126	0,0043839137	0,0043992460		-0,0127558488
		Force	-0,0000055266	0,0015646436	-0,0000307463	0,0001981120	0,0001738706		0,0003185912
		as.factor (Kniewinkel)155	-0,0008397635	0,0090437009	0,0020972770	0,0098850500	0,0055375280		-0,0040790555
		as.factor (Kniewinkel)180	-0,0012217650	0,0144221851	-0,0069079310	0,0055155514	-0,0011431150		0,0134027823
		force:as.factor (kniewinkel)155	0,0000354461	-0,0005953537	-0,0000248333	-0,0001618154	-0,0002881973		0,0003446257
		force:as.factor (kniewinkel)180	0,0000559693	-0,0009286988	0,0001259462	-0,0001761724	0,0000459133		0,0005244193
		Likelihood-ratio	1,4973240000	4,9515940000	0,5065739000	0,3048531000	2,8415300000		1,1112240000
		p-value	0,4730000000	0,0841000000	0,7762000000	0,8586000000	0,2415000000		0,5737000000

LVL	RGT	RRF	LBF	LST	RST	RBF	RVM	RVL
0,0103659600		0,0001054528	0,0004903844	-0,0121205200	0,0821861500	0,0413153700	0,0036232820	
7,0268570000		0,3648577000	1,0786020000	10,4098300000	12,5768500000	24,6428600000	12,7983400000	
0,0080000000		0,5458000000	0,2990000000	0,0013000000	0,0004000000	<.0001	0,0003000000	
0,0038985578		-0,0012416981	0,0009697696	-0,0119782000	0,0526990240	-0,0015448690	-0,0016695271	
0,0003284463		0,0000688897	-0,0000245227	-0,0000070957	0,0015173070	0,0021657530	0,0002696071	
3,0433120000		15,3665500000	0,8293416000	0,0095291730	105,71130000	119,92250000	39,1523800000	
0,0811000000		0,0001000000	0,3625000000	0,9222000000	<.0001	<.0001	<.0001	
0,0027239510		-0,0001338558	0,0001126000	-0,0120387630	0,0828928800	0,0369537490	0,0028880290	
0,0050504400		0,0000067638	0,0008417628	0,0019154400	0,0000829779	0,0048614480	0,0003642838	
0,0195397070		0,0008203274	0,0003926698	-0,0022212250	-0,0022757440	0,0085412830	0,0019140527	
29,9877700000		7,4288640000	2,4818380000	6,3000530000	0,5275649000	4,1469510000	8,9543010000	
<.0001		0,0244000000	0,2891000000	0,0429000000	0,7681000000	0,1257000000	0,0114000000	
-0,0034029922		-0,0016569410	0,0005901419	-0,0117374200	0,0531535825	-0,0042628410	-0,0025481514	
0,0003209547		0,0000712440	-0,0000233320	-0,0000143500	0,0015135706	0,0020973770	0,0002644415	
0,0046729741		0,0002805456	0,0008122354	0,0019140020	-0,0003217275	0,0038878380	0,0009795283	
0,0193104441		0,0009478262	0,0003586530	-0,0022619700	-0,0008533322	0,0086204450	0,0020172395	
30,2815500000		7,9018110000	2,4074480000	6,3253160000	0,1219955000	6,7438560000	8,4758690000	
<.0001		0,0192000000	0,3001000000	0,0423000000	0,9408000000	0,0343000000	0,0144000000	
0,0080640253		-0,0015038430	0,0001642609	-0,0117835600	0,0510626100	-0,0039134699	-0,0003300171	
-0,0002631401		0,0000646656	-0,0000018812	-0,0000117535	0,0016040100	0,0020817829	0,0001531865	
-0,0088741529		0,0004459699	0,0012363410	0,0019061980	0,0000858212	0,0065508441	-0,0004616933	
-0,0029937738		0,0001401075	0,0012592380	-0,0020979010	0,0052982910	0,0039849698	-0,0027662083	
0,0006770498		-0,0000101829	-0,0000224320	0,0000002306	-0,0000016219	-0,0001361357	0,0000671358	
0,0011395315		0,0000390352	-0,0000448351	-0,0000090468	-0,0002785311	0,0002295085	0,0002397000	
7,5880840000		1,2664760000	0,4558104000	0,0030061750	0,8496319000	0,8414484000	8,9247130000	
0,0225000000		0,5309000000	0,7962000000	0,9985000000	0,6539000000	0,6566000000	0,0115000000	

Conf	Model	MUSCLE / VARIABLE	LGT	LRF	LGL	LGM	LSL	LTA	LVM
AP	*Model 1*	Intercept	0,0025681680	-0,0065770670	0,0176661400	0,0083745620	0,0007045922		0,0256822000
		Likelihood-ratio	6,9095860000	8,4174870000	18,0039300000	7,8963680000	0,0820196600		12,9224800000
		p-value	0,0086000000	0,0037000000	<.0001	0,0050000000	0,7746000000		0,0003000000
	Model 2	Intercept	0,0022150020	-0,0107784151	0,0064846600	-0,0036039521	0,0040223150		0,0032135120
		Force	0,0000178156	0,0002149779	0,0005651400	0,0005866418	-0,0001687590		0,0011700500
		Likelihood-ratio	0,6399732000	6,2438410000	13,1099400000	9,5101170000	0,7285118000		22,2992700000
		p-value	0,4237000000	0,0125000000	0,0003000000	0,0020000000	0,3934000000		<.0001
	Model 3	Intercept	0,0021685460	-0,0079477059	0,0172040499	0,0104397170	0,0028884832		0,0273652280
		as.factor (Kniewinkel)155	0,0001378117	0,0001148952	0,0013201418	-0,0026289010	-0,0007300465		-0,0038043620
		as.factor (Kniewinkel)180	0,0010040732	0,0032787818	0,0001578583	-0,0045305500	-0,0065097896		-0,0014676520
		Likelihood-ratio	5,5058340000	4,3322740000	0,2081000000	1,2795600000	3,2164720000		0,5562788000
		p-value	0,0637000000	0,1146000000	0,9012000000	0,5274000000	0,2002000000		0,7572000000
	Model 4	Intercept	0,0018300510	-0,0119505132	0,0062426847		0,0058310345		0,0055008020
		Force	0,0000166287	0,0002226249	0,0005701127		-0,0001595791		0,0011745980
		as.factor (Kniewinkel)155	0,0001459312	-0,0004590530	0,0010608015		-0,0004757883		-0,0051827980
		as.factor (Kniewinkel)180	0,0010216520	0,0027633443	-0,0005201600		-0,0062179614		-0,0022438280
		Likelihood-ratio	5,8377230000	5,3417600000	0,2541687000		3,1352890000		1,2749520000
		p-value	0,0540000000	0,0692000000	0,8807000000		0,2085000000		0,5286000000
	Model 5	Intercept	0,0020574690	-0,0139357306	0,0092352456		0,0164796039		0,0037752571
		Force	0,0000045369	0,0003251536	0,0004000424		-0,0007292650		0,0012590768
		as.factor (Kniewinkel)155	-0,0000149147	0,0033805515	0,0065549253		-0,0172680595		0,0044147935
		as.factor (Kniewinkel)180	0,0005041676	0,0047167584	-0,0106084399		-0,0174755234		-0,0062834253
		force:as.factor (kniewinkel)155	0,0000086327	-0,0001976088	-0,0002751775		0,0009029981		-0,0004709874
		force:as.factor (kniewinkel)180	0,0000272515	-0,0001034666	0,0005501163		0,0006591226		0,0001968366
		Likelihood-ratio	0,4508220000	1,2875220000	4,3271480000		3,5298960000		1,5978530000
		p-value	0,7982000000	0,5253000000	0,1149000000		0,1712000000		0,4498000000

LVL	RGT	RRF	LBF	LST	RST	RBF	RVM	RVL
0,0244160800	0,0001379847	0,0598061400	0,0344243000	0,1022253000	-0,0080915550	-0,0007165183	0,0024220270	0,0087137850
9,4732160000	0,8341303000	13,2473400000	11,8354100000	18,8160200000	3,1922840000	1,6385970000	11,8004900000	10,7066500000
0,0021000000	0,3611000000	0,0003000000	0,0006000000	<.0001	0,0740000000	0,2005000000	0,0006000000	0,0011000000
0,0114193448	0,0003682878	0,0245603470	0,0128833870	0,0445274090	-0,0092823730	-0,0012091870	0,0010157590	0,0047908340
0,0006835515	-0,0000114338	0,0017808750	0,0011130920	0,0029654540	0,0000599204	0,0000244656	0,0000706929	0,0001971303
15,3681000000	0,8944383000	##############	50,5837500000	58,3477100000	10,7270200000	1,9976530000	13,6350900000	13,5836100000
0,0001000000	0,3443000000	<.0001	<.0001	<.0001	0,0011000000	0,1575000000	0,0002000000	0,0002000000
0,0232803790	0,0002722954	0,0614723530	0,0272535300	0,0874295200	-0,0082087099	-0,0005576565	0,0021414784	0,0076581902
-0,0021251530	-0,0002390256	-0,0012105960	0,0035770400	0,0111723400	0,0002183132	-0,0001174376	0,0004124783	0,0007510653
0,0058901760	-0,0001641751	-0,0037336100	0,0173825300	0,0303198500	0,0001423223	-0,0004022263	0,0004563202	0,0025947148
6,2468470000	1,0927150000	0,8593478000	39,4911200000	13,2152800000	0,2810408000	1,7098230000	1,9876590000	6,5462050000
0,0440000000	0,5791000000	0,6507000000	<.0001	0,0014000000	0,8689000000	0,4253000000	0,3702000000	0,0379000000
0,0118156411	0,0005041650	0,0254849410	0,0083452070	0,0277712300	-0,0095018310	-0,0010624740	0,0007856215	0,0032975496
0,0006046643	-0,0000116346	0,0017895290	0,0010070850	0,0029996880	0,0000602724	0,0000239381	0,0000694443	0,0002114075
-0,0022063611	-0,0002386762	-0,0003836706	0,0033665050	0,0127371940	0,0002666730	-0,0000839127	0,0003828555	0,0009090000
0,0058413685	-0,0001572440	-0,0028562600	0,0159355530	0,0325749670	0,0003837389	-0,0003656077	0,0004068729	0,0029191999
6,5262390000	1,1399000000	1,0036250000	44,2406800000	18,7389200000	1,5559560000	1,5859540000	1,7817370000	8,3599680000
0,0383000000	0,5656000000	0,6054000000	<.0001	0,0001000000	0,4593000000	0,4525000000	0,4103000000	0,0153000000
0,0103777600	0,0003028645	0,0277972854	0,0130863000	0,0230470470	-0,0090448160	-0,0008600708	0,0018175190	0,0043666800
0,0006758316	-0,0000013272	0,0016733950	0,0007771746	0,0032329200	0,0000360127	0,0000124166	0,0000172368	0,0001584555
0,0043639710	0,0002927305	-0,0030067620	0,0030933540	0,0215741400	0,0000213676	-0,0001900276	-0,0011466100	-0,0000441364
0,0039168120	-0,0000468597	-0,0072356482	0,0047893650	0,0387879480	-0,0007791436	-0,0009970803	-0,0007677303	0,0008909835
-0,0003315785	-0,0000265261	0,0001321322	0,0000099204	-0,0004367440	0,0000129234	0,0000078197	0,0000793082	0,0000465221
0,0000944653	-0,0000059052	0,0002173824	0,0005389405	-0,0003053280	0,0000611684	0,0000327551	0,0000570986	0,0000999242
1,5171790000	0,9197901000	0,4440565000	4,5436970000	0,3007586000	3,8293510000	0,7357884000	3,7707850000	0,6290464000
0,4683000000	0,6313000000	0,8009000000	0,1031000000	0,8604000000	0,1474000000	0,6922000000	0,1518000000	0,7301000000

Conf	Model	MUSCLE / VARIABLE	LGT	LRF	LGL	LGM	LSL	LTA	LVM
SA	*Model 1*	Intercept	0,0000990243	-0,0056735340	0,0222699600	0,0475830100	0,0688583800	0,0007769135	-0,0092561580
		Likelihood-ratio	3,8965320000	5,3505870000	9,1054740000	15,7799800000	11,4219900000	5,0198290000	9,7167980000
		p-value	0,0484000000	0,0207000000	0,0025000000	0,0001000000	0,0007000000	0,0251000000	0,0018000000
	Model 2	Intercept	0,0000445000	-0,0047254570	0,0138194757	0,0161488750	0,0529290692	0,0001420477	-0,0093618070
		Force	0,0000026773	-0,0000481680	0,0004442833	0,0015970330	0,0008186172	0,0000323127	0,0000054661
		Likelihood-ratio	0,1656193000	1,4510550000	41,7108900000	51,0520600000	28,2863300000	7,1023950000	0,0034543370
		p-value	0,6840000000	0,2284000000	<.0001	<.0001	<.0001	0,0077000000	0,9531000000
	Model 3	Intercept	0,0000000000	-0,0073705170	0,0221753015	0,0344375230	0,0700653268	0,0012392678	-0,0113081636
		as.factor (Kniewinkel)155	0,0002812700	0,0018664140	0,0009934107	0,0035242860	-0,0005766209	0,0002015907	-0,0002148445
		as.factor (Kniewinkel)180	0,0000315180	0,0035199120	-0,0005342426	0,0383297120	-0,0027460835	-0,0003407780	0,0064215420
		Likelihood-ratio	5,6921540000	19,5765300000	1,7951980000	71,8505900000	1,0108800000	2,9438000000	18,6722900000
		p-value	0,0581000000	0,0001000000	0,4075000000	<.0001	0,6032000000	0,2295000000	0,0001000000
	Model 4	Intercept		-0,0064948180	0,0136645216	0,0067483400	0,0544248445	0,0005264335	-0,0120930300
		Force		-0,0000434005	0,0004642617	0,0014197610	0,0007895060	0,0000335028	0,0000403538
		as.factor (Kniewinkel)155		0,0018411610	0,0010333297	0,0048631840	-0,0006207211	0,0002666190	-0,0002072004
		as.factor (Kniewinkel)180		0,0034747050	-0,0015284950	0,0359253700	-0,0019636055	-0,0002535127	0,0064342540
		Likelihood-ratio		19,4982800000	4,0022610000	79,1858800000	0,4259923000	0,6256268000	18,9068400000
		p-value		0,0001000000	0,1352000000	<.0001	0,8082000000	0,7314000000	0,0001000000
	Model 5	Intercept		-0,0058634770	0,0137235700	0,0169049118	0,0519644000	-0,0000567825	-0,0080126512
		Force		-0,0000741367	0,0004626636	0,0008913498	0,0009198889	0,0000616330	-0,0001619748
		as.factor (Kniewinkel)155		0,0021799750	0,0003581991	-0,0060514492	0,0083645560	0,0013533480	-0,0087712677
		as.factor (Kniewinkel)180		0,0013096920	-0,0012968980	0,0115605968	-0,0013650330	0,0004065337	0,0025397118
		force:as.factor (kniewinkel)155		-0,0000179559	0,0000343581	0,0005727994	-0,0004504824	-0,0000530571	0,0004239062
		force:as.factor (kniewinkel)180		0,0001076510	-0,0000153884	0,0012646411	-0,0000498646	-0,0000310254	0,0001964456
		Likelihood-ratio		2,3425760000	0,1121426000	8,1108650000	2,0764800000	2 6.25817	5,2967900000
		p-value		0,3100000000	0,9455000000	0,0173000000	0,3541000000	0,0438000000	0,0708000000

LVL	RGT	RRF	LBF	LST	RST	RBF	RVM	RVL
-0,0148341700		-0,0031843170	0,0145306800	0,0299086000	0,0315204400	0,0119624100	-0,0096438310	-0,0103661100
11,2689200000		14,6088600000	13,3980800000	11,3290100000	8,1269690000	7,3001730000	12,8088200000	10,5306600000
0,0008000000		0,0001000000	0,0003000000	0,0008000000	0,0044000000	0,0069000000	0,0003000000	0,0012000000
-0,0093489178		-0,0014841030	0,0034803982	0,0002193564	0,0265059920	0,0111709800	-0,0057384474	-0,0073932850
-0,0002811314		-0,0000862477	0,0005447817	0,0015163974	0,0002570639	0,0000409842	-0,0001979092	-0,0001499790
9,8890030000		8,5903660000	20,9195700000	64,1734200000	13,3700300000	1,0143460000	10,3752700000	5,2779150000
0,0017000000		0,0034000000	<.0001	<.0001	0,0003000000	0,3139000000	0,0013000000	0,0216000000
-0,0197552730		-0,0036264380	0,0116650090	0,0195367200	0,0297447294	0,0107682277	-0,0110253370	-0,0105139490
0,0057039750		-0,0001812010	0,0008771757	0,0055283940	0,0005570539	0,0006208267	0,0001227520	-0,0014981020
0,0091703380		0,0014526720	0,0092776567	0,0242596870	0,0047152283	0,0037881522	0,0037557930	0,0018516800
34,7381200000		12,3884700000	14,0932900000	40,6832100000	17,6104300000	14,1316700000	14,1335500000	6,1040120000
<.0001		0,0020000000	0,0009000000	<.0001	0,0001000000	0,0009000000	0,0009000000	0,0473000000
-0,0151895436		-0,0021828750	-0,0004171569	-0,0063697840	0,0259545940	0,0092874970	-0,0070611390	-0,0075244970
-0,0002298489		-0,0000717909	0,0005757688	0,0013596590	0,0002009652	0,0000679885	-0,0002003601	-0,0001509800
0,0056646187		-0,0002690243	0,0014626148	0,0056223950	0,0002876562	0,0007051621	-0,0000852789	-0,0014459450
0,0089613727		0,0014399580	0,0104588697	0,0223174440	0,0045892751	0,0042756480	0,0039266870	0,0018104290
36,5723500000		10,5131800000	17,2993200000	43,7406200000	14,6787600000	14,8112200000	14,5048500000	6,0913420000
<.0001		0,0052000000	0,0002000000	<.0001	0,0006000000	0,0006000000	0,0007000000	0,0476000000
-0,0113555342		-0,0016808870	0,0065131861	0,0108111600	0,0270760300	0,0114185300	-0,0011499129	-0,0045570310
-0,0004160636		-0,0000997472	0,0002184047	0,0004449351	0,0001448740	-0,0000123602	-0,0004934331	-0,0002806349
0,0023805343		-0,0002479225	-0,0058455446	0,0059750290	0,0023964550	0,0007074657	-0,0054400115	-0,0031666540
0,0007262911		-0,0003512971	-0,0026255159	-0,0110675800	0,0009518418	-0,0010920540	-0,0065889087	-0,0041437520
0,0001569088		0,0000025518	0,0003672356	-0,0000963546	-0,0000992323	-0,0000192352	0,0002474433	0,0000403321
0,0004044100		0,0000955501	0,0007150543	0,0018734930	0,0001738497	0,0001990780	0,0005345241	0,0002836770
6,5604270000		3,3207410000	7,3810950000	38,8374700000	4,0885750000	4,6878030000	11,8254000000	2,5198100000
0,0376000000		0,1901000000	0,0250000000	<.0001	0,1295000000	0,0960000000	0,0027000000	0,2837000000

Conf	Model	MUSCLE / VARIABLE	LGT	LRF	LGL	LGM	LSL	LTA	LVM
SP	*Model 1*	Intercept		0,0371285900	-0,0009804157	-0,0018771890	-0,0199837400	0,1372435000	0,0317311200
		Likelihood-ratio		10,0292000000	0,4030593000	0,6540477000	5,8289240000	18,0933800000	20,8875300000
		p-value		0,0015000000	0,5255000000	0,4187000000	0,0158000000	<.0001	<.0001
	Model 2	Intercept		0,0303354532	-0,0042020489	-0,0097181797	-0,0180697900	-0,0237210050	0,0110443800
		Force		0,0003471112	0,0001610379	0,0003965494	-0,0000967711	0,0082227570	0,0010576600
		Likelihood-ratio		9,0660060000	11,5642500000	37,5980500000	1,8544240000	125,85110000	46,99373000
		p-value		0,0026000000	0,0007000000	<.0001	0,1733000000	<.0001	<.0001
	Model 3	Intercept		0,0376022892	-0,0005268616	0,0003400553	-0,0178785380	0,1602979900	0,0299478170
		as.factor (Kniewinkel)155		-0,0011556680	-0,0003868277	-0,0020673663	-0,0025694700	-0,0281145900	-0,0022263770
		as.factor (Kniewinkel)180		-0,0002459054	-0,0009530507	-0,0054457432	-0,0036605590	-0,0403167200	0,0087078790
		Likelihood-ratio		0,1906271000	3,7450820000	10,0813400000	8,0363260000	15,5650700000	10,9338600000
		p-value		0,9091000000	0,1537000000	0,0065000000	0,0180000000	0,0004000000	0,0042000000
	Model 4	Intercept		0,0308185468	-0,0034049907	-0,0079768369	-0,0159116934	0,0055570930	0,0101852640
		Force		0,0003624029	0,0001794448	0,0004074398	-0,0001069094	0,0083996790	0,0010292460
		as.factor (Kniewinkel)155		-0,0019091250	-0,0014630782	-0,0017334398	-0,0024684882	-0,0343025590	-0,0024376630
		as.factor (Kniewinkel)180		-0,0004064174	-0,0019806539	-0,0048678986	-0,0033264626	-0,0626219600	0,0077609580
		Likelihood-ratio		0,5201511000	7,7157180000	10,4172400000	8,7997340000	33,0111000000	11,8434400000
		p-value		0,7710000000	0,0211000000	0,0055000000	0,0123000000	<.0001	0,0027000000
	Model 5	Intercept		0,0324375600	-0,0057650766	-0,0089644630	-0,0192655600	-0,0370751217	0,0187870356
		Force		0,0002853597	0,0003154482	0,0004575280	0,0000526275	0,0105972540	0,0005845074
		as.factor (Kniewinkel)155		-0,0053170930	0,0012996478	-0,0022961530	0,0014306380	-0,0188670140	-0,0083559059
		as.factor (Kniewinkel)180		-0,0021659020	0,0022815357	-0,0019762390	0,0035533850	0,0326031749	-0,0113841673
		force:as.factor (kniewinkel)155		0,0001616927	-0,0001620437	0,0000306207	-0,0001875369	-0,0007938045	0,0003215915
		force:as.factor (kniewinkel)180		0,0000831588	-0,0002384390	-0,0001616900	-0,0003302351	-0,0048947402	0,0009803484
		Likelihood-ratio		0,3417753000	9,5823310000	1,7004860000	6,7939160000	18,0457600000	7,9431960000
		p-value		0,8429000000	0,0083000000	0,4273000000	0,0335000000	0,0001000000	0,0188000000

LVL	RGT	RRF	LBF	LST	RST	RBF	RVM	RVL
0,0487753200		0,0248856600	-0,0005430525	0,0002764411	-0,0016271780	-0,0025140340	0,0256451700	0,0346898100
20,7342800000		16,7326000000	0,2264619000	0,3667947000	2,5253760000	4,9848770000	19,6089200000	18,3003100000
<.0001		<.0001	0,6342000000	0,5448000000	0,1120000000	0,0256000000	<.0001	<.0001
0,0278977610		0,0114385146	-0,0015003530	-0,0002915978	-0,0026024681	-0,0024839830	0,0129240970	0,0149974218
0,0010653140		0,0006917882	0,0000483001	0,0000286688	0,0000493816	-0,0000014847	0,0006451230	0,0009958141
25,34479000		36,5099700000	2,8599850000	3,0570670000	8,2933730000	0,0024373220	27,0841600000	46,7476700000
<.0001		<.0001	0,0908000000	0,0804000000	0,0040000000	0,9606000000	<.0001	<.0001
0,0393141769		0,0216476630	0,0000191683	0,0002535184	-0,0014504211	-0,0026724531	0,0257194020	0,0302774020
0,0007543085		0,0014646650	-0,0004972921	-0,0002646578	-0,0006350200	-0,0002681214	-0,0022285100	-0,0027616570
0,0285885333		0,0090224900	-0,0013343130	0,0003710958	0,0002072971	0,0008593497	0,0021656150	0,0173882330
49,9819400000		17,3000500000	4,5765520000	2,6023320000	6,0930000000	2,8756220000	3,9803250000	47,7226000000
<.0001		0,0002000000	0,1014000000	0,2722000000	0,0475000000	0,2374000000	0,1367000000	<.0001
0,0050144854		0,0083931232	-0,0008620172	-0,0002831056	-0,0025286520	-0,0032321470	0,0101444170	0,0108595560
0,0015648896		0,0006705161	0,0000430125	0,0000279702	0,0000516952	0,0000250921	0,0007308450	0,0010154030
0,0008040721		0,0008844442	-0,0004816548	-0,0003102244	-0,0006147635	-0,0002838805	-0,0020957590	-0,0027921030
0,0399359811		0,0103630030	-0,0012538780	0,0003672668	0,0003958502	0,0010572810	0,0056263340	0,0152401840
69,3358000000		29,8137000000	4,1538870000	2,8271610000	9,1319610000	3,9742140000	10,5789800000	62,7114900000
<.0001		<.0001	0,1253000000	0,2433000000	0,0104000000	0,1371000000	0,0050000000	<.0001
0,0298926179		0,0171030000	-0,0009577512	-0,0003546332	-0,0020157630	-0,0037347120	0,0089617860	0,0134335700
0,0004646294		0,0002514593	0,0000486574	0,0000341583	0,0000264306	0,0000511118	0,0007871435	0,0008937207
-0,0021189090		-0,0068093749	-0,0007147221	0,0001290492	-0,0009632879	0,0009470757	0,0018808270	-0,0007923528
-0,0063633728		-0,0029935368	-0,0006775042	0,0000737903	-0,0007743854	0,0014293420	0,0044688220	0,0063003680
0,0001658731		0,0003672433	0,0000107874	-0,0000238374	0,0000175060	-0,0000620504	-0,0001976384	-0,0000935525
0,0018122561		0,0006325594	-0,0000308717	0,0000085114	0,0000592204	-0,0000209074	0,0000680224	0,0004183241
19,2388900000		10,5592900000	0,4211088000	0,7915135000	3,1315400000	1,6274870000	1,0590710000	3,7930590000
0,0001000000		0,0051000000	0,8101000000	0,6732000000	0,2089000000	0,4432000000	0,5889000000	0,1501000000

Conf	Model	MUSCLE / VARIABLE	LGT	LRF	LGL	LGM	LSL	LTA	LVM
VD	*Model 1*	Intercept		0,0019280340	0,0018685830	0,0056923600	0,0107623800	0,0008798749	0,0053091200
		Likelihood-ratio		13,1266000000	9,9959570000	14,1527300000	11,2144100000	6,8172810000	13,4424100000
		p-value		0,0003000000	0,0016000000	0,0002000000	0,0008000000	0,0090000000	0,0002000000
	Model 2	Intercept		0,0006383686	0,0017017460	0,0034273510	0,0109712571	0,0006765422	-0,0010867394
		Force		0,0000644296	0,0000085816	0,0001186194	-0,0000108585	0,0000104338	0,0003238912
		Likelihood-ratio		1,5914060000	1,8543290000	7,6600140000	0,0876136500	2,1260270000	14,7281600000
		p-value		0,2071000000	0,1733000000	0,0056000000	0,7672000000	0,1448000000	0,0001000000
	Model 3	Intercept			0,0017619350	0,0035341380	0,0103954462	0,0006960942	0,0009622445
		as.factor (Kniewinkel)155			0,0002463282	0,0031615490	0,0006262614	0,0003334757	0,0112501169
		as.factor (Kniewinkel)180			0,0000985892	0,0039112300	0,0005734693	0,0002581756	0,0030237498
		Likelihood-ratio			2,7679020000	25,9431300000	0,7887086000	5,6229260000	34,4787600000
		p-value			0,2506000000	<.0001	0,6741000000	0,0601000000	<.0001
	Model 4	Intercept			0,0015948100	0,0015650818	0,0105620000	0,0004828040	-0,0062037097
		Force			0,0000086667	0,0001102469	-0,0000079266	0,0000108626	0,0003559108
		as.factor (Kniewinkel)155			0,0002367548	0,0030456119	0,0005977305	0,0003359647	0,0116851044
		as.factor (Kniewinkel)180			0,0001034524	0,0035639940	0,0005558901	0,0002608243	0,0031335573
		Likelihood-ratio			2,6438740000	27,1320800000	0,7426179000	5,7497340000	39,5800300000
		p-value			0,2666000000	<.0001	0,6898000000	0,0564000000	<.0001
	Model 5	Intercept			0,0018260330	0,0039161110	0,0045602110	0,0007003834	0,0008266111
		Force			0,0000000000	0,0000000000	0,0000000000	0,0000000000	0,0000000000
		as.factor (Kniewinkel)155			0,0003262848	-0,0002544740	-0,0024369330	0,0002125421	-0,0059470580
		as.factor (Kniewinkel)180			-0,0006668837	-0,0001543118	-0,0002854732	-0,0002501940	-0,0001884350
		force:as.factor (kniewinkel)155			-0,0000125353	0,0001613702	0,0007498150	0,0000064936	0,0010069420
		force:as.factor (kniewinkel)180			0,0000373624	0,0001737496	0,0004857342	0,0000255448	0,0001027741
		Likelihood-ratio			12,4054000000	5,7135960000	4,7652240000	2,2042880000	32,0672400000
		p-value			0,0020000000	0,0575000000	0,0923000000	0,3322000000	<.0001

LVL	RGT	RRF	LBF	LST	RST	RBF	RVM	RVL
0,0082212100				0,0002586898			0,0022338320	
10,0114100000				5,7499220000			7,7868440000	
0,0016000000				0,0165000000			0,0053000000	
0,0051480122				0,0001800704			-0,0002751534	
0,0001568796				0,0000039707			0,0001297725	
5,7628190000				0,2606096000			8,8132080000	
0,0164000000				0,6097000000			0,0030000000	
0,0061197226							0,0006893691	
0,0067880941							0,0027557735	
0,0000200281							0,0021604092	
45,3619200000							9,8921580000	
<.0001							0,0071000000	
0,0034359529							-0,0016768763	
0,0001370643							0,0001248387	
0,0067014240							0,0027615305	
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